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Factors affecting foraging by breeding farmland birds

Kathryn A. Murray (BSc. Hons, MSc)

**A thesis submitted in fulfilment of the requirements of the Open
University for the degree of Doctor of Philosophy.**

**Harper-Adams University College in collaboration with the Allerton
Research and Educational Trust.**

2004

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ABSTRACT

Factors affecting foraging by breeding farmland birds

This thesis investigates nesting success, foraging behaviour, chick diet and growth of three ecologically contrasting species (skylark *Alauda arvensis*, yellowhammer *Emberiza citrinella* and song thrush *Turdus philomelos*) on farmland, in relation to microhabitat and the availability of invertebrates. Fieldwork was conducted on a lowland mixed arable farm in Leicestershire over the breeding seasons 2000 - 2002. Telemetry was used to monitor adult song thrushes and fledgling skylarks. Skylark nest density was highest in set-aside and lowest in crops, yellowhammer nest density was greatest in herbaceous vegetation and field margins whilst song thrush nest density was greatest in hedgerows and woodland. Birds did not utilise the available habitat at random for nesting. Provisioning skylarks and yellowhammers utilised managed set-aside strips more than would be expected, although both foraged in cereals. Song thrushes foraged primarily in woodland and boundary habitats, avoiding cereal crops, permanent pasture and set-aside. The largest cause of nest failure for each study species was predation. Skylark nest survival improved with increasing vegetation density at the nest site. Yellowhammer nest survival was affected by temperature and rainfall. Song thrush nest survival was affected by predator control, nest site location on the farm and habitat. Skylarks selected sparse vegetation and bare ground when foraging in winter cereals. Each species selected some invertebrate taxa over others, independently of chick age. Skylarks and yellowhammers did not forage in sites with greater invertebrate abundance than others, but song thrushes tended to forage in habitats with higher invertebrate biomass. Skylark chick growth rates were positively influenced by set-aside and negatively by spiders in the diet and the proportion of 'other habitats' around the nest. Skylark chicks with higher growth rates were more likely to fledge. No habitat effects or environmental factors were found to affect song thrush chick growth rates. Tagged skylark chicks exhibited a low post-fledgling survival rate, with most predated whilst flightless. This thesis identified actual and potential conservation benefits for nationally declining skylark, yellowhammer and song thrush populations arising from the management of cropped and non-cropped habitats.

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I dedicate this thesis to my family

My father,
My mother,
My sisters,
My brother-in-law,
My nieces,
And Malcolm.

X.

Declaration

This thesis is the work of, and has been written by, the author. No part of this work has been submitted for any other degree or professional qualification.

Kathryn. A. Murray

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Publications

Murray, K.A., Wilcox, A., & Stoate, C. (2002) A simultaneous assessment of farmland habitat use by breeding skylarks and yellowhammers. In *Birds and Agriculture* (eds N.D. Boatman, N. Carter, A.D. Evans, P.V. Grice, C. Stoate & J.D. Wilson), Vol. 67, pp. 121-127. *Aspects of Applied Biology*, Edinburgh.

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Peach, W.J., Robinson, R.A. & Murray, K.A. (2004). Demographic and Environmental Causes of the Decline of Rural Song Thrushes *Turdus philomelos* in lowland Britain. (2004). *Ibis*: submitted.

CHAPTER 1

INTRODUCTION

Introduction

The first part of this chapter provides a brief overview of changes in agricultural practices and how they have impacted on the abundance of farmland birds. The review concentrates mainly on lowland arable farming, although it briefly highlights other farming systems where they are specifically relevant to this thesis. Recently, much has been written on the effects of agricultural intensification on wildlife and the information presented pertains mainly to O'Connor & Shrubbs (1986); Fuller et al. (1991); Fuller et al. (1995); Rackham (1995); Stoate (1995, 1996); Pain & Pienkowski (1997); Fuller (2000); Chamberlain et al. (2000a); Robinson & Sutherland (2002b); Donald et al. (2002b). The second part of the chapter introduces the study site, the study species (skylark (*Alauda arvensis*), yellowhammer (*Emberiza citrinella*) and song thrush (*Turdus philomelos*)) and the aims of this thesis.

1.1 The importance of farmland for birds

Farmland covers approximately 18.3million ha (70 - 75%) of the total land area in Britain (Milton, 1994; Robinson and Sutherland, 2002). Cereals cover approximately 3.3 million ha (DEFRA statistics available at <http://www.defra.gov.uk/esg>), which is roughly 16 times more than the combined areas of local and national nature reserves in the UK (Potts, 1991). Lowland farmland provides breeding or wintering habitats for nearly 120 bird species of European conservation concern (SPECs), the largest number of such species supported by any habitat (Tucker & Heath, 1994). Over half the bird species associated with farmland in Britain today are of conservation interest (Tucker, 1997).

Over the past 30 years farming practices have changed dramatically, faster than any other time in the history of agriculture, with radical effects on wildlife and the environment. The declines of most farmland birds started during the mid to late 1970s, and agricultural intensification is widely recognised as playing a role in reductions in abundance (e.g. Fuller et al., 1995; Campbell et al., 1997; Siriwardena et al., 1998a; Chamberlain et al., 2000a; Siriwardena et al., 2001). Interestingly, species that specialise on farmland in Britain have declined more rapidly, on average, than most habitat generalists (Siriwardena et al., 1998a). A farmland specialist is defined as 'a species that either nests in fields or relies on fields or field margins significantly for its food'

(Fuller et al., 1995; Fuller, 2000). Farmland in Europe also holds 60% of all bird SPEC species, even though many of these species were once formerly common and widely distributed (Tucker & Heath, 1994).

When birds are viewed as environmental indicators of the 'health' of our countryside, it is apparent from the severe decline in populations of farmland birds that modern farming methods must change if the declines are to be reversed. In the UK, the Government pledged to reverse or stem the declines of 20 common farmland specialists by 2020, thereby recognising the decreases as a scientific and public concern (Gregory et al., 2000). Agricultural intensification has also reduced the diversity and abundance of arable weeds and invertebrates (Campbell et al., 1997), which constitute a large part of the diet of many species, contributing to farmland bird declines.

1.2 Historical changes in British agriculture

When the last of the ice sheets disappeared around 8000BC, woodland covered most of Britain. Farming in Britain began in the early Neolithic (circa 4000BC) and this coincided with the clearance of small areas of forests (Rackham, 1995). However as early as the Roman invasion in 43AD, so much forest area had been removed that it covered as many parts of southern Britain as it does today (Rackham, 1995). Exceptions included the Fenland of East Anglia and the Sedgemoor levels of Somerset and Lancashire mosses, which still had to be drained successfully. The Domesday book, in 1086, shows that England was not a well-wooded area and most of England consisted of farmland with 'islands of wood'. Agriculture serves to select and domesticate important plant and animal species for food. The increasing demands for food, as a result of growing populations over the centuries, were met by putting such species on land formerly occupied by forest, shrubs, grasses etc (Wood et al., 2000).

Farming systems developed and were slowly refined over hundreds of years, allowing most wildlife to adapt to changes from predominantly woodland to open farmland. Simple crop rotations were originally used to control weeds and disease and to maintain soil fertility. Basic rotations consisted of a three-field system with winter corn, spring corn and fallow, spreading labour throughout the year. Animals were kept to work the land and

also to provide food and manure to fertilise the soil. Fields were generally open and the animals were watched over by men.

During the sixteenth century, high wool prices led to an increase in sheep farming, resulting in the widespread change of arable land to pasture. The Enclosure Act of the eighteenth century allowed fences and hedges to separate and secure fields; the basis of many field boundaries and hedgerows observed today (O'Connor & Shrubbs, 1986). Further hedgerows were established during the Agricultural Revolution of the eighteenth and nineteenth century to act as wind breaks on plains in addition to enclosing fields. Field size was generally small and most farm systems were still rotational and mixed. In the nineteenth century a standard four-course crop rotation was used, the 'Norfolk four-course rotation': a root crop for 'cleaning weeds' (e.g. swedes and turnips, which also fed cattle) in the first year, followed by cereals (e.g. oats, spring barley), then nitrogen fixing grasses or legumes (i.e. through undersowing within the cereal crop) to improve soil fertility and then cereals again (e.g. wheat). By this time much land was now farmed with horses and ploughs, and men hoed between the rows of sown crop to control weeds.

Cereal prices rose during much of the late eighteenth and nineteenth century, which in turn led to an increase in arable land throughout Britain. Farmers were protected from cheaper grain prices abroad by Corn Laws that prevented imports into the country and maintained corn prices until 1846. In the 1880s prices fell due to cheap, high quality cereal imports from places such as America. The price of wool also fell due to cheap imports from New Zealand, soon leading to a fall in the price of lamb and mutton, with which British farmers could not compete. Vast improvements in transport networks, particularly with refrigerated steam ships in the 1870s, and the doctrine of free trade exacerbated the situation. Furthermore, the population demands for grain were now too high for Britain to meet and half the wheat consumed was imported. Following declines in cereal prices, an agricultural depression ensued that continued into the 1930s. Consequently, large areas of fertile agricultural land were taken out of production and abandoned, so by 1930 - 1932 81% of agricultural land was under grass. 1.18million ha of crops and grass (excluding rough grass) in England and Wales were taken out of production, between 1916 and 1940, and 0.87million ha were lost from agriculture altogether. Approximately 77% of this land lost went to urban and industrial use (O'Connor & Shrubbs, 1986).

Following the Second World War (1938 – 45), when Britain was almost ‘starved into submission’, there was a drive for self-sufficiency in the production of food and an increased standard of living. This ended the depression. The post-war 1947 Agricultural Act introduced widespread price maintenance for crops, and capital grants and subsidies to encourage investment in agriculture. It was concerned only with food production and consequently, farming methods intensified from the 1950s through to the present day. This has resulted in an increase in arable land, leading to a dramatic change from the generally mixed farming landscape present at the beginning of the 20th century. Arable farming now predominates in the east of Britain, with lighter soils, lower rainfall and better drainage. Pastoral farming is pre-dominant in the west.

So successful was this drive for increased food production that by the mid - 1980s there were large surpluses of food (Milton, 1994). Britain entered the European Community (EC) in 1973 (then the European Economic Community or EEC - established in 1957 under The Treaty of Rome), hence joining the Common Agricultural Policy (CAP). The CAP guaranteed fixed agricultural product prices and established a threshold level below which the EU became a buyer, taking the produce out of the market and storing it. The CAP also forced levies on cheaper imports and granted export ‘refunds’ to allow excesses to be traded competitively on the world market. Farmers were guaranteed income for their produce and this in turn led to specialisation and over-production. Capital grants were available through the EU, enabling farmers to become mechanised, hence driving intensification and encouraging the removal of many non-agricultural habitats that are likely to benefit biodiversity (MacDonald & Johnson, 2000).

Mechanisation reduced the number of farm labourers required to work the land. In 1930, 630,000 people were employed in agriculture and this fell to 196,000 in 1981, despite the increase in the total area of farmland (O'Connor & Shrubbs, 1986). The number of tractors in service increased from 20,000 in 1930 to 400,000 in 1960 and the use of combine harvesters rose from zero in the 1930s to over 70,000 in 1981. These machines were able to carry out several tasks in succession, such as preparing the seedbed, spraying, fertilising and planting. This heavy reliance on farm machinery thus not only reduced the amount of labour required but also reduced the number of working farm animals, such as horses and oxen. As a result, less hay and oats were grown to feed the few working farm animals, and those crops were replaced with silage. Silage fields were

planted with grass varieties such as Ryegrass (*Lolium perenne*), cocksfoot (*Dactylis glomerata*) and clovers (*Trifolium spp*), which depend on frequent cutting and fertilising to provide a first-class winter feed.

Farms were amalgamated in response to the benefits associated with economies of scale. From 1875 to 1979 the average farm size increased by a factor of 2.0 – 2.5 (O'Connor & Shrubbs, 1986). Today, 10% of the largest farms produce over half of the total food crop in the UK (Curry, 2002). Land drainage and the removal of hedgerows, copses, woodland and non-cropped habitats facilitated the use of large machinery and helped increase yields. The increased field sizes, often ploughed up to the base of the hedge, allowed huge areas of the same crop types to be grown, contributing to a homogenous, simplified environment. Approximately 50% of Britain's hedgerows have been removed since 1947 (Barr & Parr, 1996), drastically changing the face of the countryside. New cereal crop strains were developed that were more disease resistant and hardy. This together with autumn sowing allowed earlier harvesting and increased yields. The amount of spring-sown crops subsequently declined, as did their associated winter stubbles. In the 1950s, the majority of cereals were spring sown but by the mid – 1990s only approximately 10% were (Evans, 1997).

The use of combine harvesters and grain dryers also dramatically improved the efficiency of harvesting crops and their subsequent storage. Far less grain was therefore available, both in stubble fields and farmyards, which formed an important dietary component of many granivorous passerine species over winter. The use of tractors and ploughs allowed land to be quickly prepared for the sowing of the next crop. Thus land could be cropped for almost the entire year, again discouraging areas of winter stubble.

Pesticide use, (insecticides, herbicides, fungicides, molluscides) to control invertebrate pests, weeds and diseases, increased on farmland from the 1950s, doubling in use every 10 years (Campbell et al., 1997). Today, cereal crops receive an average of 10 pesticide applications. With farming polarisation, many farms no longer kept farm animals that could provide them with a source of organic fertiliser. Inorganic fertilisers, such as phosphorus, nitrogen and potassium, replaced farmland manure and bone meal, and the amounts applied over the course of a crop season increased to enhance crop growth and yield. As a consequence, undersowing cereal crops with leys to increase soil fertility declined. Traditional mixed arable crop rotations also declined since the

need to have small workable fields had disappeared, and the use of machinery and pesticides ensured a good crop yield, whilst fertilisers maintained soil fertility year after year.

The increases in pesticide usage had detrimental effects on much wildlife (Potts, 1991; Wilson, 1992; Campbell et al., 1997; Potts, 1997; Donald, 1998). Many early insecticides were not target-specific, causing a general reduction in invertebrates that could benefit the crop, such as predatory arthropods, and potential chick food resources. Some broad-spectrum insecticides and herbicides affect target and non-target species, for example the organophosphates dimethoate, phosalone and pyrethroid deltamethrin (Aebischer & Potts, 1990; Sotherton, 1990), but continue to be widely used. Selective insecticides, such as pirimicarb, a specific aphicide, are generally better for the cereal ecosystem since they do not affect the abundance of most non-target invertebrate groups. However, broad-spectrum insecticides are often applied as a prophylactic, whereas herbicides and fungicides are mostly applied in response to disease or weed thresholds (with the exception of residual herbicides). Fungicides were introduced in the 1970s (Stoate, 1996; Fuller, 2000) and the improved control of crop diseases led to fewer farms sowing break crops, such as turnips and beans, again contributing to simplified farm landscape. The increased use of herbicides also greatly reduced the diversity and abundance of arable weeds. However, some common weed species, such as Black-grass (*Alopecurus myosuroides*), have become resistant to the herbicides used to control them so that only broad-spectrum products, such as glyphosphate, are now effective (Stoate, 1996).

As discussed, the main changes in agriculture took place relatively quickly following the Second World War. The majority of arable farms in Britain are now 'conventionally' farmed, adopting intensive management techniques. Fewer farms are organic or 'traditionally' mixed (arable and livestock), maintaining habitat diversity through larger crop rotations, smaller field sizes and more non-cropped habitats. Agricultural intensification is higher in the EU than in non-EU countries because it is driven by the price-support policies. Farmland bird declines were reported to be significantly greater in western EU countries than eastern communist countries from 1970 – 1990 (Donald et al., 2001c). Currently, there are 15 member states in the EU. Ten eastern European countries and three Mediterranean countries will be invited to join the EU from May 2004. When this happens, it is conceivable that these countries will also experience a rapid loss of biodiversity in the same way that western countries have, with much detriment to their wildlife and environment (Vickery,

2001; Donald et al., 2002b). Although the rate of intensification has slowed in recent years, the negative effects on farmland birds need to be rectified. In order to do this, the causes of species decline must be fully understood so that appropriate conservation measures can be put in place.

1.3 Farmland bird declines

Agricultural habitats have the highest overall species richness of any other habitat (Baillie et al., 1997; Tucker, 1997); probably due to the area and diverse range of habitats they cover. Across Europe, extensive farming systems generally support higher bird species diversity and abundance than that of intensively managed land (Stoate et al., 2003). Cereals dominate arable land cover, being the most important crop, providing 60% of the world's food (Potts, 1997). In Europe, cereals cover an area greater than the British Isles and in the UK alone cereal crops cover 17% of the land surface (Potts, 1997). Severe declines in farmland birds are well documented and the Government has responded to these declines by committing to Biodiversity Action Plans (BAPs) to conserve particular species and habitats (Anon, 1995; Gibbons et al., 1996; Anon, 1998). BAPs establish quantifiable targets to be achieved by a certain date. There are currently 10 BAPs for previously common and widespread farmland bird species; grey partridge (*Perdix perdix*), skylark, linnet (*Carduelis cannabina*), corn bunting (*Miliaria calandra*), stone curlew (*Burhinus oediconemus*), turtle dove (*Streptopelia turtur*), corncrake (*Crex crex*), tree sparrow (*Passer montanus*), song thrush and bullfinch (*Pyrrhula pyrrhula*). Monitoring is an essential component of the BAPs, so that changes in conservation status can be detected. Habitat management is also key to conserving many species and within arable and horticultural habitats the BAP objectives and targets are: to protect arable areas for wildlife from improper land use or intensification, to oppose conversion of semi-natural habitats to arable and to maintain, improve and restore by management the diversity of 15,000 ha of cereal fields margins by 2010 (Haines-Young et al., 2000).

In Britain, the Common Bird Census (CBC) commenced in 1962. The CBC served to monitor the breeding bird populations of over 200 plots in lowland Britain each year, by mapping territories (Marchant et al., 1990), of which almost half are on farmland. Population trends of 32 farmland bird species (26 specific to farmland) were determined, from CBC data from 1973 to 1994. 21 species (19 specific to farmland) were shown to have declined in abundance, (Campbell et al., 1997), coinciding with agricultural intensification from the mid 1970s

(Fuller et al., 1995; Siriwardena et al., 1998a; Chamberlain et al., 2000a). Species closely associated with farmland that declined included tree sparrow, grey partridge, corn bunting, turtle dove, lapwing (*Vanellus vanellus*), skylark, linnet and yellowhammer. A few species, namely the woodpigeon (*Columba palumbus*), stock dove (*Columba oenas*) and collared dove (*Streptopelia decaocto*), have increased on farmland from 1973 to 1994 (Campbell et al., 1997), probably due to increases in the amount of oilseed rape being sown. In 1994 the Breeding Bird Survey (BBS) was implemented (after a two-year pilot study), which recorded breeding birds more systematically over 1x1km plots of the national grid across the UK, and after several years overlap took over from the CBC in 2000. Both the CBC and BBS infrequently monitor rarer bird species, due to their absence or scarcity from monitored sites.

On a larger scale, breeding bird species distribution trends can be assessed using data collected from the occupancy of 10-km squares from two breeding bird atlases (1968 – 1972, Sharrock, 1976; 1988 – 1991, Gibbons et al., 1993). The percentage change in distribution between the time periods of the two atlases has shown a range contraction for many farmland bird species. This method of assessing changes in range can be coarser than that of the CBC. For example, skylark distribution range showed only a small contraction (–2%), from occupancy data of 10-km squares (Gibbons et al., 1993), most likely because of the wide variety of open habitats in which they occur. This contraction did not reveal the 58% decrease in skylark abundance over the same time period, 1988 – 1991, recorded by the CBC. Nonetheless, breeding bird atlases are good for assessing large-scale patterns of bird distributions and changes (Donald & Fuller, 1998). Indeed, for example, ciril bunting (*Emberiza cirilus*) contracted in range by 83%, although the Common Bird Index did not detect this, since ciril buntings were too scarce to be monitored by this scheme.

Farming practices that are most likely to cause farmland bird declines are briefly discussed here and, in more detail, in Fuller (2000) and Robinson & Sutherland (2002a), although different factors involved in agricultural intensification affect species differently (Chamberlain et al., 2000a). The simplified cropping patterns reduce habitat heterogeneity thus affecting invertebrate abundance, weed diversity and foraging and nesting opportunities. The massive reduction in hedgerows nationwide has affected bird species richness and abundance. Hedge height and width can influence which species use this habitat (Green & Griffiths, 1994). Ploughing up to the hedge base removes grassy field margins and rough vegetation, which are important for

some species to nest and forage (Arnold, 1983; Parish et al., 1995; Stoate et al., 1998; Perkins et al., 2002), and reduces habitat diversity further. Grassy field margins are richer in invertebrate abundance and diversity than within the crop (Thomas & Marshall, 1999), although they are affected by pesticide and fertiliser spray drift. The switch from spring to autumn sowing also reduces the availability of winter stubbles, which many granivorous bird species utilise during the winter for food, possibly decreasing over-winter survival. Also, unlike autumn sown cereals, spring cereals allow more skylark breeding attempts to be made per season because crops do not become too tall for nesting (Wilson et al., 1997a; Chamberlain & Crick, 1999).

Pesticide use can affect birds directly, by causing their death, or indirectly, by reducing the amount of potential food available (invertebrates, weeds and seeds) (Campbell et al., 1997; Wilson et al., 1999; Burns, 2000; Morris, 2002). Both effects have the potential to reduce breeding or wintering populations. The grey partridge is the best-researched example of the indirect effects of pesticides on a farmland bird species. The GCT detected the grey partridge decline early because of its economic value as a game bird. Their long-term study, spanning over 30 years, demonstrated that pesticides could limit the supply of suitable invertebrate chick food items. In the case of the grey partridge, herbicides killed invertebrate host plants thus reducing invertebrate chick food availability. This was compounded by the use of insecticides that subsequently caused chicks to die from starvation and hence reduced the breeding population (Rands & Sotherton, 1986; Potts, 1991). Ewald & Aebischer (1999) found that partridge density was inversely related to the number of herbicide applications and positively linked to the number of weed taxa. They also showed the abundance of chick food invertebrate groups and their host plants was negatively related to insecticide and herbicide use respectively. A more recent investigation into the indirect effects of pesticides on farmland birds provided evidence from autecological studies of the effects of insecticides on the abundance of invertebrate prey taxa for yellowhammer and corn bunting. Insecticides significantly affected their prey abundance, foraging behaviour and chick growth, and for the corn bunting, also chick survival (Morris, 2002).

During the late 1980s and early 1990s, there was much publicised concern about the effects of agricultural intensification on wildlife, habitat diversity and particularly farmland bird declines across Europe. From this concern stemmed many studies examining the range, contraction, abundance and ecology of several key declining farmland bird species within the UK; such as corn bunting (Donald et al., 1994; Brickle, 1999), ciril bunting (Evans et al., 1997), corncrake - (Tyler et al., 1998; Green & Gibbons, 2000), tree sparrow (Siriwardena

et al., 1998a; Anderson et al., 2002), skylark (Chamberlain & Gregory, 1999; Donald, 1999), yellowhammer (Kyrkos et al., 1998; MacCleod, 2001), whitethroat (*Sylvia communis*) - (Siriwardena et al., 1998a; Stoate et al., 2001), lapwing (Sheldon, 2002), linnet (Moorcroft and Wilson 2000), house sparrow (*Passer domesticus*) - (Hole et al., 2002), swallow (*Hirundo rustica*) (Evans et al., 2003) and turtle dove (Browne & Aebischer 2004).

Agricultural changes that may have contributed to the declines in arable farmland bird populations are listed in Table 1, adapted from Fuller (2000). Other factors that may contribute to declines are disease and severe winters (Fuller et al., 1995; Peach et al., 1999), although these factors would also be expected to affect populations other than farmland species in other habitats.

1.4 Declines of farmland plants and invertebrates

Agricultural intensification has resulted in the decline of invertebrate or plant food resources for many farmland bird species (Aebischer, 1991; Wilson, 1992; Wilson & Aebischer, 1995; Wilson et al., 1999; Sotherton & Self, 2000). In his study site in Sussex, Aebischer (1990) reports declines of invertebrates in cereals fields of 50% every ten years. Historically, over 700 arable weed species would have been found in cereal fields alone in western and central Europe (Potts, 1991), but with the increased use of pesticides in the past few decades, arable weeds and many invertebrate species have declined (Aebischer, 1991; Wilson, 1992; Campbell et al., 1997; Donald, 1998; Ewald & Aebischer, 1999). Consequently, arable farmland may now hold a higher number of Red Data listed plant species than any other habitat in the UK (Rich & Woodruff, 1996; Donald, 1998). Unlike the bird monitoring schemes that are in place, there are few schemes designed to monitor long-term trends in invertebrate and weed abundance (Campbell et al., 1997; Donald, 1998), especially on farmland.

For example, the Rothamsted Insect Survey (RIS) started in the early 1960s and uses light traps and 12.2m high suction traps to catch macrolepidoptera and migrating aphids respectively in order to monitor populations. Traps also catch other insect groups, which are used to assess changes in abundance. The Butterfly Monitoring Scheme began in 1976 and transects are used to monitor butterfly populations. The GCT Sussex Downs study started in 1970 and covers an area of 62km² including 100 farms. The GCT study monitors invertebrates, using

suction sampling, and arable weeds each year in June, thus enabling long-term population trends to be established. Results have shown that some invertebrate groups have increased over the period of intensification, whilst many have declined. Aphids, the most commonly targeted pest species, are likely to have increased through the unsystematic use of pesticides, thereby reducing the numbers of their natural predators, as have collembola. Nonetheless, some predatory arthropods have been fairly resilient to pesticides and remain common, e.g. some carabids (Donald, 1998). Grass weed species, such as Black-grass (*Alopecurus myosuroides*), are also more resilient to herbicides and are increasing in abundance when other less resilient, less common arable weed species are declining (Wilson, 1992). Selective pesticide use has demonstrated positive results for the abundance of chick-food invertebrates and diversity of broadleaved weeds (Sotherton, 1991). Lutman et al. (2003) discuss selective weed management and the relationship between competitive effects (i.e. those affecting crop yields and quality) and the benefits for birds and invertebrates (food and shelter) in the arable ecosystem.

Within crops, the number and diversity of arable weeds has decreased with the application of inorganic fertiliser use (Wilson, 1992; Marshall et al., 2003). The new fertilisers encourage rapid and uniform growth of the crop, perhaps leaving little room or light for the growth of arable weeds (Sotherton & Self, 2000). The removal of non-cropped habitats, the practice of ploughing up to hedgerow bases, land drainage and increased use of pesticides have caused declines in arable weeds and invertebrate species (Wilson & Aebischer, 1995; Wilson et al., 1999). Plant diversity is greatest at the cereal edge (generally up to the first 4m), and diversity of seeds and seedlings decreases further from the crop edge in both autumn and spring sown cereals. Therefore, agri-environment schemes implementing field margins and conservation headlands around cereal crops may help to increase the diversity and abundance of many declining arable weed species and their associated invertebrate fauna.

Table 1: Key trends in arable farming intensification that contributed to the declines of farmland bird populations. Taken and adapted from Fuller (2000).

Factor	Trend	Causes	Implications
<i>Mechanisation</i>	Increasing use of machinery since the 1950s	Hedgerow removal and ploughing of non-cropped habitats to increase field sizes, yields and to facilitate large machines. Facilitated autumn sowing of crops, thus leading to a reduction in winter stubbles Efficiency of harvesting increased with the use of combines Large-scale application of pesticides and fertilisers	Reduction in habitat heterogeneity, associated declines in invertebrate and arable weed species Reduction in winter food sources, possibly leading to reduced over-winter survival rates. Less split grain as a food source during the winter months. Can reduce invertebrate and arable weed/seed resources available to birds Removes nesting and foraging opportunities for many species.
<i>Fertilisers</i>	Huge increase in the use of inorganic fertilisers such as nitrogen at the expense of farmyard manure (FYM)	Fast growing, dense crops Reduction in mixed rotations since crops can be grown continuously, without break crops Reduction in FYM inputs on cultivated fields	Removal of suitable nesting vegetation structure for ground nesting birds Reduction in short sparse vegetation and bare ground suitable for foraging Reduction in habitat heterogeneity Reduction in break crops being sown FYM can increase earthworm abundance. Reductions may affect invertebrate feeding birds
<i>Pesticides</i>	Increasing application of synthetic herbicides, insecticides, molluscicides and fungicides	Direct effects evident in the past with the use of organochlorines Most pesticides can reduce potential food resources for birds (both invertebrate, weed and seed)	Birds ate seed dressings and died. Declines in some raptor populations with DDT etc. Can lead to reduced survival rates of chicks and adults during the breeding season and over winter.
<i>Simplification in crop rotations</i>	Move from mixed farming to simpler rotations	Reduction in habitat heterogeneity, leading to a homogenous environment Reduction in the sowing of leys in cereals Move to autumn sowing of crops	Reduction in suitable nesting sites for multiple nesters across a breeding season. Breeding requirements may not be met across the breeding season, in terms of food, so birds may have to shift territories or finish breeding early. Reduction in important chick food invertebrate taxa, such as earthworms and sawfly larvae. Reduction in winter stubbles, associated with spring crops. Reduction in bare cultivated land in spring for foraging.

1.5 Measures to reduce agricultural intensification

Currently, the cost of storage of surplus food is approximately €3billion annually, which is almost as much as that budgeted for agri-environment schemes and other measures to reverse the effects of intensification (Donald et al., 2002b). It was the financial burden of storing surplus food and paying subsidies that led to the 1992 CAP reform, to address issues such as over production and the environment. Consequently, measures to reduce production support and replace it with new or improved direct payment to farmers were introduced (i.e. Arable Area Payments – AAPs to compensate farmers for cuts in price support). In 1993, the Integrated Administration Control System (IACS) was introduced as part of the CAP reform, which made it compulsory for farmers to record all details of their farm on a 1:2500-scale map to claim AAPs. This enables an inclusive land-use map to be made annually, so changes in farmland habitats can potentially be closely monitored.

However, from 1st January 2005 a Single Farm Payment Scheme (SFPS) will be introduced, which will replace AAPs (EC Regulation 1782/2003 from the ‘mid-term review’ of CAP, 26th June 2003), decoupling direct aid and production (www.defra.gov.uk/farm/capreform). Farmers will receive a single payment based on historical production receipts, from 2000-02, removing the incentives to over-produce. The SFP ‘entitlements’ will be payable to whoever is occupying ‘agricultural’ land in 2005, and any agricultural land taken up by arable or permanent pasture in England is eligible. The land itself does not have to be connected to present or future production and it has to be at the claimants ‘disposal’ for a period of at least 10 months between 1/10/04 to 28/2/06 (see www.andersons.co.uk for details). To receive these direct payments farmers must ‘cross comply’ and meet certain standards concerning environmental, food safety, animal health and welfare standards.

Set-aside was first introduced as a voluntary scheme in 1988, which paid farmers to take land out of production, with the aim of reducing the amount of cereal production. In 1992, acceptance of set-aside became compulsory to qualify for AAPs and between 5 - 18% of farmed land every year since has been taken out of production. An unplanned potential benefit of this scheme for wildlife, in particular farmland birds, is the production of suitable areas for foraging and nesting for many species (Firbank et al., 1993).

There are two types of set-aside. Non-rotational set-aside is taken out of production on a long-term basis for 5 years or more and rotational set-aside is taken out of production for one year only. The set-aside land is either left to regenerate naturally or is sown with a green crop cover to prevent nitrogen leaching. It must, however, receive specific management to achieve maximum benefits for wildlife (Wilson & Fuller, 1992; Sotherton et al., 1994; Wilson et al., 1995; Potts, 1997); it receives little or no pesticide applications, it cannot be harvested and it must be mown at the end of the summer (mid-July to mid-August) to control weeds. From 1995, a 'flexible' set-aside option allowed farmers to place set-aside where they chose and it could be split into strips at least 20m wide and 0.3ha in area or left as whole fields. In 2002, the area of set-aside in England was 702,635ha (http://farmstats.defra.gov.uk/cs/farmstats_data).

There are four options for non-rotational set-aside – natural regeneration, field margins and strips, Wild Bird Cover (WBC) and grassland. Two common WBC options on set-aside are cereal set-aside (CSA), which provides brood rearing cover for game birds and kale set-aside (KSA), which provides winter cover for game birds. Mixtures sown must be unharvestable, with at least two crops other than legumes (Sotherton et al., 1994; Sotherton, 1998). Songbirds make use of the cover and winter food source, (Brickle, 1997; Stoate & Szczur, 1997) and invertebrates and mammals also benefit from the food supply and vegetation cover (Boatman & Bence, 2000).

As a result of the introduction of compulsory set-aside, the production of surplus food requirements is falling and the percentage of arable land being taken out of production each year is decreasing. Although set-aside was introduced primarily as a production control, limited pesticide use and other restricted agricultural practices on set-aside benefit plant, invertebrate and bird communities by increasing diversity and abundance (Sotherton et al., 1994; Wilson et al., 1995; Evans, 1997; Vickery & Buckingham, 2001). Managed set-aside is likely to benefit more farmland bird species than unmanaged set-aside (Sotherton, 1998), although this is at a direct cost to the farmer. From 2005 farmers will no longer receive direct payment or subsidies for set-aside or production, and to recoup farm income losses, they will have to incorporate some agri-environment options on their farms to supplement income under the currently piloted Entry Level Scheme (ELS) in England (see section 1.5.1). Under the SFPS (replacing the AAPS) all land claimed in 2005, other than permanent pasture and exclusively organic holdings, will have a set-aside requirement. The new set-aside period will run from January 15th to

September 1st. Farmers with a set-aside obligation (producer threshold over 19.48ha) must claim their set-aside entitlements before claiming their SFP (www.defra.gov.uk/farm/capreform). Recent changes in minimum area and strip widths (from 10 to 5m) will mean set-aside can be placed along field margins, maximising biodiversity benefits through the provision of food and habitat for farmland and hedgerow birds and by protecting water quality. Energy crops will also be able to be grown on set-aside contributing to renewable energy sources. Modulation (which redirects a proportion of CAP direct subsidies to agri-environment and other Rural Development Programmes) will help fund this. Presently, however, a whole suite of agri-environment scheme options that have been developed and tested for wildlife benefits across the country is available on a voluntary basis to many farmers.

1.5.1 Agri-environment schemes

Agri-environment schemes encourage farmers to receive payment to manage land sympathetically for wildlife, and are likely to lead to environmentally sensitive changes in farming practice (Chamberlain et al., 1999a). Currently 26 out of 44 European countries have schemes in place (Kleijn and Sutherland, 2003). All schemes are regularly monitored and evaluated, although their evaluations could be more robust (Kleijn and Sutherland, 2003). Their benefits are discussed by Ovenden et al. (1998). In the UK, some schemes involving changes in farming practices have shown that farmland bird declines can be reversed locally for some species. These include grey partridge, mediated by reduced pesticide use and provision of nesting cover (Potts, 1986), circl bunting, by the provision of over-winter stubbles and grass margins (Evans, 1997), corncrake, by the provision of nesting cover and the delay in harvesting grass for fodder (Tyler et al., 1998) and stone curlew, by providing adjacent fields of spring crops and grazed pasture (Green & Griffiths, 1994) – also see Aebischer et al., (2000) for a review. In the last few years, increasing numbers of farmers have been seeking advice on managing their land for wildlife and conservation (MacDonald & Johnson, 2000). Several organisations, both statutory and non-statutory, are now available to provide advice to farmers on the best ways to farm in order to minimise the effects of intensification on bird populations and other wildlife (e.g. ARET – The Allerton Research and Educational Trust; ADAS – Agricultural Developmental Advisory Service; DEFRA - Department of the Environment For Rural Affairs; FWAG – Farming and Wildlife Advisory Group; GCT – Game Conservancy Trust; LEAF – Linking the Environment and Farming; RSPB – Royal Society for the Protection of Birds).

Currently the two main agri-environment schemes in England are Environmentally Sensitive Areas (ESAs) and the Countryside Stewardship Scheme (CSS), now supported by the England Rural Development Programme (ERDP), following the CAP reform Agenda 2000. However, by 2005 it is hoped a single scheme available to all farmers in England that adopts a 'whole farm approach' will replace these schemes (Curry, 2002). The 'Entry Level Scheme' (ELS) is presently being piloted across four areas in England (Anon 2003), and since it is a pilot scheme, and as yet not widely available, is discussed in detail in Chapter 7. However, if it is successful it is envisaged that the ELS will be fully introduced as the 'Environmental Stewardship Scheme' (ESS) in 2005 and will be key to maximising habitat heterogeneity on a much wider scale.

Environmentally Sensitive Areas: In 1987, this scheme was the first of the agri-environment schemes. To date there are 22 ESA's in England, covering 10% of agricultural land (MAFF, 2000c). ESAs are parts of the countryside, designated as being of particularly high landscape, wildlife, archaeological or historic value, that are threatened by changes in farming practice (e.g. the Lake District).

Countryside Stewardship Scheme: The voluntary Countryside Commission grant scheme was launched as a pilot scheme in 1991 and operated throughout England outside ESAs. In 1996, MAFF (now DEFRA) took over the scheme and renamed it the Countryside Stewardship Scheme (MAFF, 2000a). CSS aims to improve, restore, create and conserve the diversity of the English countryside and improve opportunities for public access through offering payment incentives to farmers. Agreements last 10 years. Options within the scheme for arable land, that aim to re-create traditional field boundaries, such as hedgerows, banks, ditches and stone walls, will benefit many bird species (Arnold, 1983; Osborne, 1984; Green et al., 1994; MacDonald & Johnson, 1995; Parish et al., 1995; Fuller et al., 1997; Bradbury & Stoate, 2000).

New prescriptions piloted under the MAFF pilot Arable Stewardship Scheme (1998 – 2001) (MAFF, 2000) were made available in 2002 (MAFF, 2000; Anon, 2002). These included conservation headlands (CHs), beetle banks, over wintered stubbles and wildlife mixtures.

Conservation headlands are 6 - 12m wide strips along the edge of a cereal crop, where the use of insecticides and herbicides is restricted enabling broadleaved weed species and beneficial insects to survive (Aebischer &

Blake, 1994). Invertebrates are able to colonise the crop from these headlands, providing greater prey abundance and foraging sites for birds, whilst helping to control pest species such as aphididae. CHs are based on the work of the Cereals and Gamebirds Research Project, of the Game Conservancy Trust (GCT), and were first developed in the early 1980s (Sotherton 1991; Potts, 1997).

Beetle banks are earth ridges created across an arable field, and sown with tussocky grass species, producing an undisturbed sward structure (except for occasional cutting). They provide ideal nesting areas for skylarks and also breeding and foraging areas for small mammals and insects. Conditions are also ideal for invertebrates breeding and over-wintering, which will move into the crop in the summer and help control aphids (Thomas et al., 1992a; Thomas et al., 1992b; Collins et al., 2003). The provision of *overwintered stubbles* after a cereal crop harvest, followed by a spring cereal, helps to increase birds' winter foraging opportunities. *Wildlife mixtures*, namely 'Wild Bird Seed' mixtures and 'Pollen and Nectar' mixtures, sown with either 3 seed-bearing crops or at least 4 nectar-rich plants, help to increase invertebrate and plant food items during the summer and winter. This prescription is based on WBC developed on set-aside and will provide seeds required by many passerine species throughout the year. Field margins act as buffers from spray drift, protecting hedges allowing invertebrate diversity and abundance and the weed species that support them to increase. The creation of networks of grass margins, grass strips, CHs, beetle banks and hedgerows encourages increases in wild flowers and insects, and maintains habitat diversity which will benefit breeding and wintering farmland birds, insects and mammals (Bence et al., 1999; Boatman & Bence, 2000; Boatman et al., 2000; Vickery et al., 2002).

Eight more smaller agri-environment schemes are available to farmers and landowners across England, under the ERDP. Full details of each scheme are found in <http://www.defra.gov.uk>: Organic Farming Scheme, Farm Woodland Premium Scheme, Woodland Grant Scheme, Hill Farm Allowance Scheme, Rural Enterprise Scheme, Vocational Training Scheme, Energy Crops Scheme and Processing and Marketing Grants Scheme. The schemes briefly discussed below may have particular relevance to lowland farmland birds.

The Organic Conversion Scheme is available to farmers throughout England who wish to convert to organic production in accordance with the rules of the UK Register of Organic Foods Standards (UKROFS). No pesticides are applied to crops. Mechanical methods of weed-control and artificial fertilisers are avoided, often

providing a greater abundance and diversity of insects, plants and food for birds. Organic farms have been shown to support higher densities of some farmland bird species than conventional farms (Peterson, 1994; Chamberlain et al., 1999b; Wilson et al., 1997a), possibly because of the reduced amounts of pesticides used, smaller field sizes, crop rotations and greater crop and non-crop habitat heterogeneity. Currently, public demand for organically grown food outstrips the UK's production and much organic food is imported for economic reasons. The Farm Woodland Premium Scheme helps to convert agricultural land to woodland and is confined to arable land (i.e. land eligible for the AAP), improved land (i.e. improved grass and cropped land ineligible for the AAP) and improved land (i.e. land used for agriculture for at least 3 years but not meeting the other definitions). The Woodland Grant Scheme provides funds to create new woodlands and encourage the good management and regeneration of existing woodlands. The latter two schemes are likely to benefit declining non-farmland specialists, such as song thrushes, that also occupy farmland.

1.5.2 Non-scheme related management

All management that reduces the intensity of farming is likely to benefit birds, but in order to achieve this, farmers will generally require some form of compensation for forgone profits. Extensification is the opposite of 'intensification' and was first defined, in policy in 1989 (Article 4 of EC Regulation 4115/88), as 'lower inputs (fertilisers and pesticides) and outputs (yields)' on a given area of land (Anon, 1989). Extensification was a (proposed) scheme originally designed to help reduce the amount of cereals and beef reaching the market by 20% (Anon, 1989; Lack, 1992). It could have been first introduced as an arable scheme in the UK in 1985 under EC R797 Article 19, but set-aside was then introduced and the current AAP scheme does not encourage extensification (Potts, 1997). Extensification is best compared with traditional farming methods, since it requires reduced artificial inputs and allows rapid recovery of invertebrate and seed resources. However, it reduces farm income. It increases biodiversity since it serves to increase habitat diversity and quality (Evans, 1997; Potts, 1997; Wilson et al., 1999), but today is mainly practiced, and funded, in upland and livestock farming areas.

Game management, carried out by farmers with an interest in shooting, leads to the active management of land, primarily to increase the survival of game birds such as pheasant (*Phasianus colchicus*) and partridges.

Alongside the maintenance and planting of hedgerows, woodland and field margins, WBC crops are often sown. Farmers can plant WBC on set-aside but receive no additional payment to do this. The provision of grain, in game feeders or by hand, and WBC not only benefits wild game in the winter, but also encourages some seed-eating passerines to feed on the spilt grain during winter, which may increase over-winter survival and improve subsequent breeding success. For example, yellowhammers preferably foraged in triticale (WBC) early in winter, then moved to game feeders later on (Stoate & Szczur, 1997), whilst corn buntings initially foraged on stubble fields early on, then moved to game feeders and WBC strips as winter progressed (Brickle, 1997).

Predator control was once a systematic part of countryside management. Most farmers or landowners controlled pest species such as the fox (*Vulpes vulpes*), mink (*Mustela vison*) and corvids (crows *Corvus corone* and magpie – *Pica pica*), particularly as a part of game management. However, since World War Two, the decline in grey partridge numbers and the decrease in income from shooting have reduced the number of gamekeepers employed (Potts, 1997). Consequently, a decline in habitat management often followed in these areas. The number of corvids has also increased nationally with the lack of control, mostly on farmland (O'Connor & Shrubbs, 1986; Gooch et al., 1991; Gregory & Marchant, 1996). Corvids are opportunistic and will predate songbird eggs and nestlings. Increases in avian predators have been associated with the decline of many farmland bird species, although no significant relationship has yet been found with the declines in passerine abundance (Gooch et al., 1991; Thomson et al., 1998). Stoate & Thomson (2000) did find that game management (including predator control) helped increase song thrush abundance at Loddington over time and predator control alone has been shown to increase the productivity of game birds (Chesness et al., 1968; Tapper et al., 1996). Both latter studies involved removal of predators in different areas and demonstrated an increase in hatching or nesting success in those areas with predator control. Tapper et al. (1996) switched predator control on their two study areas after 3 years, for a further 3 years, and reported a significant increase in partridge nesting success and abundance on the kept area and a decrease on non-kept land. Conversely, a meta-analysis of 20 studies on predator removal as a conservation measure to increase bird populations (Côté & Sutherland, 1997) suggested that, while predator control may have a positive effect on nest survival rates and post-breeding population sizes, its effects on subsequent breeding bird populations was not significant.

1.6 Habitat selection: scales and theories.

Habitat use by breeding birds was examined on a number of levels during this study (nesting, foraging, vegetation structure, post-fledging). This section therefore aims to provide a brief and general overview of the theories associated with habitat selection. Information was taken principally from Krebs and Davies (1987, 1991), Newton (1998), Fuller (2002) and Sutherland (2002). These publications examine in detail the issue of habitat selection and provide numerous examples of important studies.

Habitat selection is defined here as the method by which an individual bird recognises its habitat, which may involve cues such as vegetation cover, food resources, weather, microclimate etc. Individual birds may show different levels and types of habitat preferences within their home range and within the landscape (Aebischer et al., 1993), but these differences may not always be apparent at a population level. Each species has basic habitat requirements to survive and reproduce and may require different habitats for different parts of their breeding and life cycle. Habitat selection operates on a range of levels: geographical, landscape, habitat patch, territory and microhabitat (see Fuller 2002).

Breeding success and survival of a species are often used as a means of quantifying habitat quality, which may be influenced by extrinsic factors such as food resources, cover, predation, interference, proximity to good feeding grounds etc. Habitat selection implies that there are 'good' and 'poor' habitats and assumes that individuals recognise the differences between them, although habitat variation occurs at different spatial scales (from differences between territories within the same area to regional differences in habitat quality) and an individual's performance is often different between habitats. On that pretext, high quality habitats would be expected to have better reproductive success and survival rates than poorer quality habitats.

Several theories are used to describe the processes by which individuals may select habitats (be it to overwinter, establish territories, nest, forage etc). The 'Ideal Free Distribution' (Fretwell and Lucas 1970) describes a theoretical distribution where there may be, for example, two habitats - one of high and one of poor quality. Individuals are 'free' to move into either habitat. Initially the higher quality habitat is filled first and there is no limit to the number of individuals that can move into it. However, as the number of individuals increase, the

amount of available resources decreases so at some point individuals will be better off moving into the lower quality habitat. Competitors therefore alter their distribution in relation to habitat quality so each individual can gain equally. The 'Ideal Despotic Distribution' theory explains that the first individuals to arrive establish themselves in the higher quality habitat and as a result of territoriality or a social hierarchy exclude others. Some individuals are therefore forced to occupy the poor quality habitat, even though they do less well there (unlike the Ideal Free Distribution). As the poor habitat fills up with territorial individuals the last arrivals may be excluded altogether and become 'floaters' (non breeding birds). This 'Buffer effect' (Brown 1969) refers to the sequential occupation of habitats, where the high and poor quality habitats are filled in order and the excluded individuals are 'on stand by' for a vacant territory. Primary habitats are thus 'buffered' against dramatic changes in numbers and the constancy of densities in the good habitat depends on the presence of birds in the nearby poor habitat. One of the best known examples of this is of work by Krebs (1971) with Great tits (*Parus major*) in Wytham woods, Oxfordshire, which showed birds in hedgerows (secondary habitat) moved to woodland (primary habitat) where breeding success was higher when territories were created by removing birds. Most bird species are however likely to follow a mixture of both the ideal free and ideal despotic theory since it is unlikely all individuals are equal competitors.

The 'source-sink' theory recognises that habitats vary in quality (on different spatial scales) and stresses the view that populations are unlikely to be self-sustaining in all areas where they are found. 'Sources' (often containing higher quality territories) produce excess individuals and these then move to 'sinks', which cannot maintain their population. 'Ecological traps' are said to exist when individuals mistake poor quality habitat as good quality habitat, resulting in a population decline. This is more likely to happen in a man-made environment when habitat indicators can be distorted, e.g. areas of crops attracting ground nesting birds whose nests are then destroyed during agricultural operations. Sutherland (2002) summarises the problems faced by these theories.

Habitat fragmentation, generally caused by mans alteration of the landscape, has resulted in (generally) small patches of semi-natural habitats being surrounded by farmland or urbanised land. The size and spacing of habitat patches suitable for specific species can affect their regional occurrence. Small habitat patches often act as sinks since they cannot support large numbers of breeding birds, which may influence breeding performance

and survival. Greater disturbance, nutrient constraints or predation pressures within small patches may affect habitat quality potentially creating sinks. Fragmentation also increases habitat edge proportions and not all birds associate with habitat edges. Furthermore, if there are large distances between suitable habitat patches (for example to nest and forage in) the size of each patch and the proximity of it to another may be important, since travelling time, energy expenditure, exposure to predators etc. would affect reproductive success. A good nesting habitat patch may be well utilised if there are sufficient foraging patches within reach. 'Multiple patch use' means parent birds have to increase their own food intake to sustain the extra energy expenditure when visiting several patches, which could lead to a decrease in delivering food or feeding young. The distance travelled to and from the nest may constrain the prey delivery rate and ultimately reduce reproductive success, and this may be further reduced if suitable foraging patches are spaced out within a territory (see Charnov 1976; Hinsley 2000).

1.7 Thesis aims and structure

This thesis investigates the foraging behaviour, habitat use, nesting success and chick diet of three ecologically contrasting lowland farmland bird species (skylark, yellowhammer and song thrush) in relation to the availability of invertebrates and vegetation structure in cropped and non-cropped habitats at Loddington. In particular, the thesis examined a number of factors that could influence the foraging ecology of each of the study species during the nesting and provisioning stage of their breeding season. A number of declining farmland bird species feed their chicks mainly or entirely invertebrates, and for some species invertebrate availability is known to influence chick survival. Habitats created on farmland to benefit wild game, such as those available at Loddington, may also provide insect rich feeding habitats for passerines.

This thesis has been structured so that each chapter concentrates on a different theme, each being readable in its own right. Figure 1 outlines the structure behind the research into 'Factors affecting foraging by breeding farmland birds'. All references are combined in a reference list at the end to avoid repetition. Research was carried out from March to the end of August 2000 – 2002.

Chapter 2 examines nest site location and nest density in relation to available habitats. Nest survival was investigated in relation to a range of different parameters; e.g. habitat, weather, diet and specific nest site characteristics. The hypothesis tested was ‘habitats available to breeding birds influences nest survival at Loddington’.

Chapter 3 examines habitat use by breeding birds, both when nesting and when provisioning young. It explores habitat composition around nest sites and foraging habitat selection. Since Loddington implemented a wide range of non-cropped habitats, and manages semi-natural habitats, the hypothesis tested was ‘birds used wildlife crops and semi-natural habitats more than commercial crops, relative to their availability’.

Chapter 4 examines vegetation structure at foraging and control sites in relation to vegetation structure, botanical species composition and invertebrate abundance. The hypothesis tested was ‘invertebrate abundance determines habitat use by provisioning birds independently of habitat structure’.

Chapter 5 assesses nestling diet in relation to invertebrate availability at foraging sites and whether this changes with age. It assesses factors that could affect chick growth rates (using mass and tarsus measurements). The hypothesis tested was ‘provisioning birds show clear selection for some invertebrate taxa over others, relative to their availability’.

Chapter 6 investigates skylark post-fledging behaviour, survival and habitat use. The aim of this chapter was to develop a methodology that could be applied to skylarks post-fledging; in order to investigate habitat use in a similar way to that for provisioning adults. The hypothesis tested was ‘newly fledged skylarks chicks use the habitat available to them non-randomly’.

Chapter 7, the final chapter, summarises all results and discusses current and future agri-environment schemes, and other habitat management options that may benefit each of the study species. Future research requirements, highlighted by the study, are suggested.

Appendix 1, Figures a, b and c (Chapter 1) show example maps of nest sites for each species and examples of defined foraging areas used in the analyses.

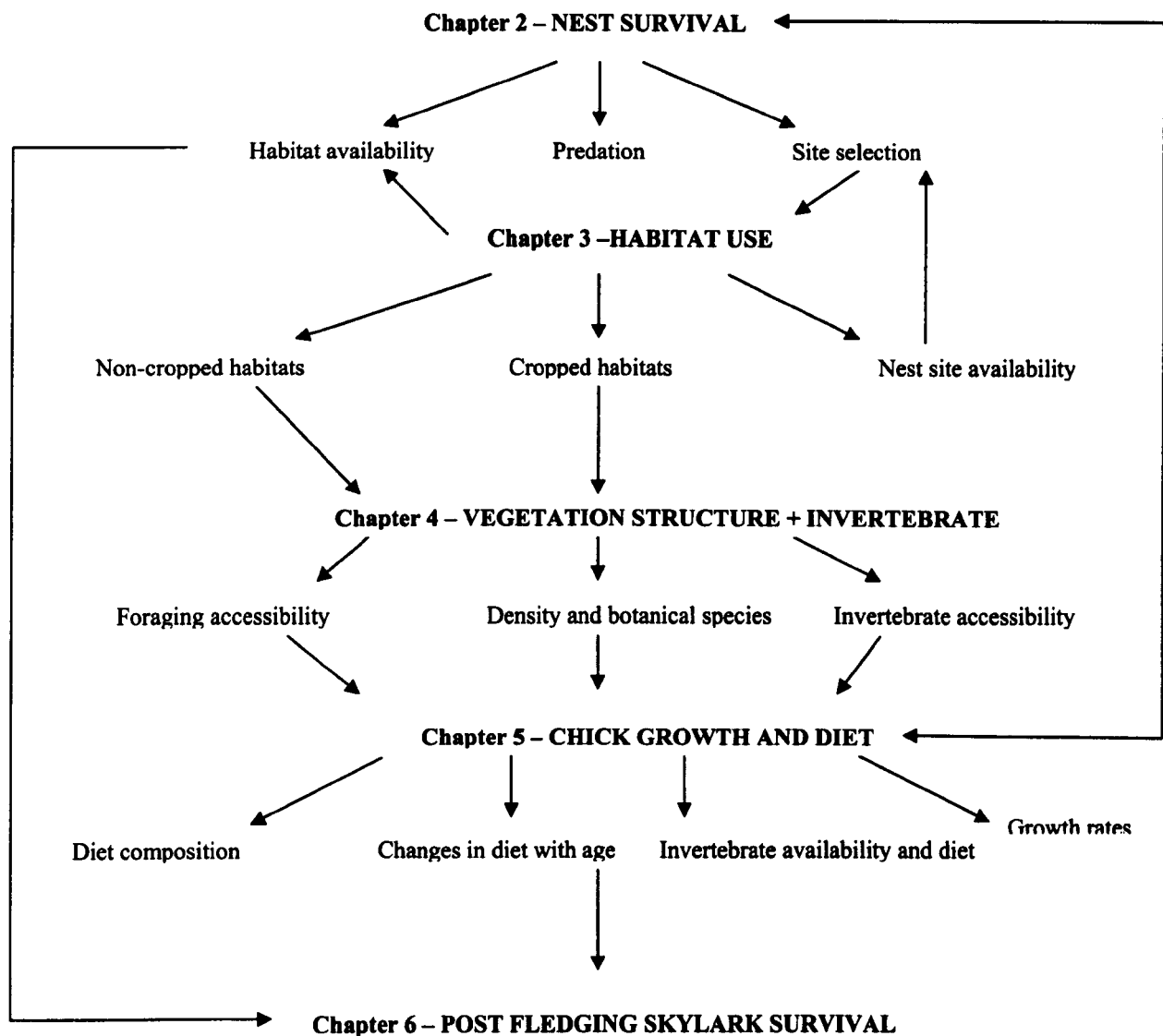


Figure 1: The structure behind the thesis's research into 'Factors affecting foraging by breeding farmland birds'.

1.8 The Study Site: Loddington

Section 1.6 is drawn largely from Boatman et al. (1999), Boatman & Bence (2000), Boatman & Stoate (2000), Boatman et al. (2000) and Stoate & Leake (2002).

In 1992, the Allerton Research and Educational Trust (ARET), in partnership with The Game Conservancy Trust (GCT), was set up to manage Loddington estate (SK789021), a 333ha mixed farm. ARET's role was to develop techniques to demonstrate how game and wildlife conservation could be integrated with profitable farming (Boatman et al., 2000). The farm was managed commercially and the research was partly supported by a trust fund, independent of the farm. Loddington is located mainly on clay soils and is predominantly arable. Sheep graze on 43 ha of permanent pasture and 28 ha is woodland including a disused railway embankment. A five-course crop rotation system is used (winter wheat, winter barley (replaced with winter oats in 2002), winter oilseed rape, winter wheat and winter or spring beans) (Figure 2). Beetle banks divide large fields, and on either side of a beetle bank a different crop is usually grown to increase crop diversity. Field boundaries at Loddington are generally well established and maintain blackthorn (*Prunus spinosa*) and hawthorn (*Crataegus monogyna*) hedgerows, most associated with ditches.

In summer, insecticides are only used when pest species exceed a threshold level (determined by the farm manager) and this has only occurred once since the project started. Pirimicarb was then used at two-thirds rate to control aphids, because it is a more selective insecticide than organophosphates or pyrethroids, with little effect on non-target invertebrate groups. No insecticides are sprayed within 6m of any crop edge, or 12m in cereals in summer, in order to protect invertebrates within these areas so they can re-colonise the rest of the field.

Within fields, between fields and at a farm level, habitat diversity was established and maintained through a number of practical conservation measures starting in 1993. Beetle banks sown with tussocky perennial grasses, conservation headlands, grassy field margins adjacent to hedgerows, and hedgerow and ditch maintenance were all implemented in order to increase the amount of chick food (invertebrates) and nest sites primarily for wild game (see Boatman et al., 2000 for a review). Set-aside was generally sown in at least 20m wide strips rather than in blocks, was non-rotational and managed, being sown mainly with different 8m wide Wild Bird Cover (WBC) kale or cereal-based mixes and beetle banks. Field-edge and mid-field set-aside strips were used to develop agri-environment scheme options for the CSS, including Wildlife mixtures and beetle banks.

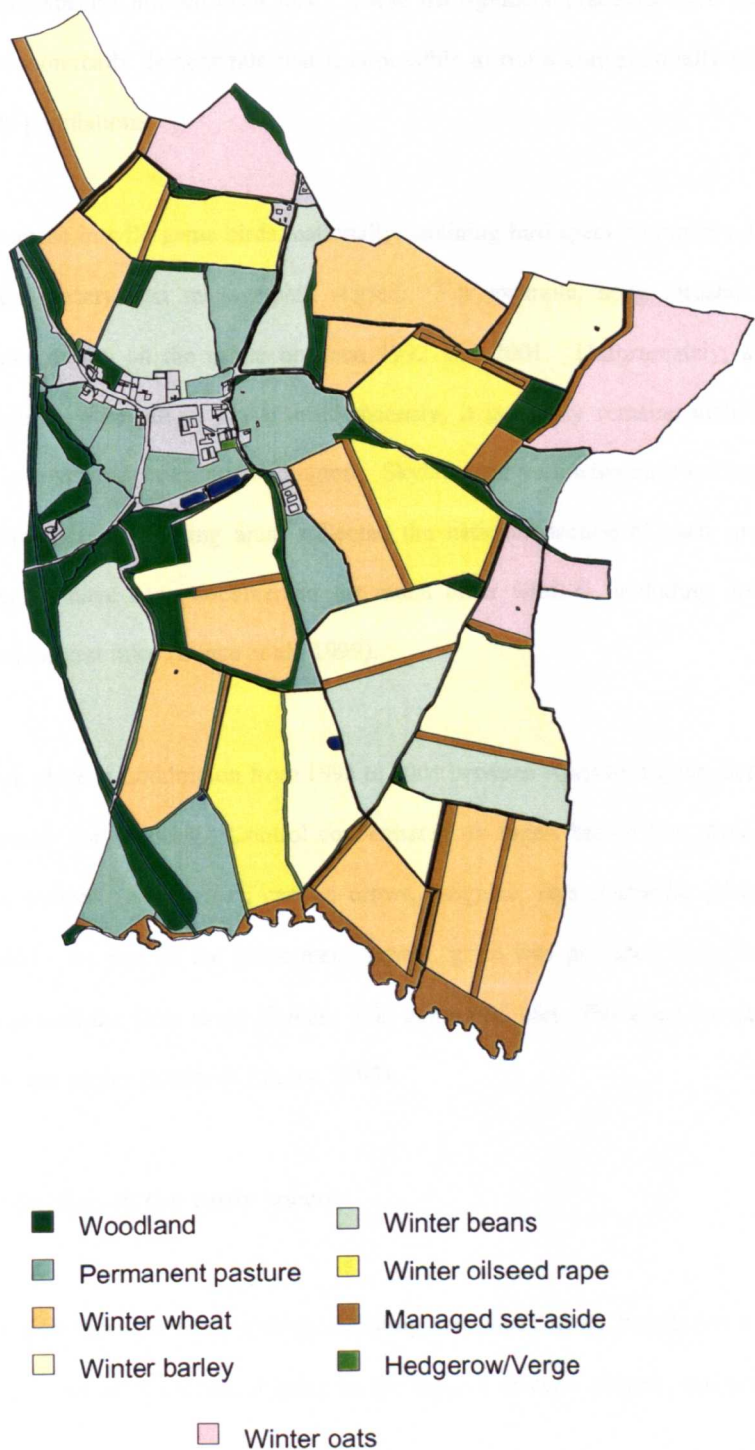


Figure 2: Loddington estate crop and habitat map (333ha) for 2001/2002.

WBC options, under set-aside, were first trialled by sowing plots with different kale and cereal seed mixtures to determine which bird species utilised each mix. These management practices have enabled Loddington to scientifically and economically demonstrate that it is possible to run a conventionally managed lowland farm and increase wildlife populations.

In addition to an increase in wild game birds, nationally declining bird species numbers dramatically increased at Loddington after conservation management started. For example, song thrushes territory abundance increased by a factor of 4.6 on the estate between 1992 and 2001. Unfortunately, as many conservation management procedures were put in place simultaneously, it generally remains difficult to identify which techniques benefit individual species at Loddington. Skylark and yellowhammer territory numbers generally remain constant, although surrounding areas reflected the national decline of each species. Benefits from research at Loddington have been documented for much other wildlife, including invertebrate abundance, butterflies, hares and harvest mice (Bence et al., 1999).

Predator control took place at Loddington from 1993 to 2001 between April to August, because of the interest in wild game management for shooting. Control concentrated on foxes, brown rats (*Rattus norvegicus*), stoats (*Mustela erminea*), weasels (*M. nivalis*), carrion crows, magpies, jays (*Garrulus glandarius*) and squirrels (*Sciurus carolinensis*). As part of the game management, grain was provided from September to March in numerous hoppers around the farm to supplement wild game bird diet. Passerine species also benefited from this food resource in the winter (Stoate & Szczur, 1997).

1.9 A brief introduction to the study species

This section briefly introduces the study species, outlining their distribution, population trends and conservation status. Further details on each species, relating to the subject of each chapter, are provided throughout the thesis.

The yellowhammer, song thrush and skylark are frequently listed as common farmland bird species. However, each species is declining both internationally and nationally (Lack, 1986; Tucker & Heath, 1994; Gibbons et al.,

1996; Hagemeyer & Blair, 1997). Both yellowhammers and skylarks are particularly susceptible to further decline as they are mainly confined to agricultural habitats, while gardens may provide the song thrush with an alternative refuge (Fuller, 2000). All three species are on the UK Red List of birds (Gibbons et al., 1996; Gregory et al., 2002). They are species of the highest conservation priority, having experienced population declines of more than 50% between 1974 and 1999. The skylark is classified as a SPEC 3 species (unfavourable conservation status in Europe due to recent declines, but with world population not concentrated in Europe) and the song thrush and yellowhammer as SPEC 4 species (favourable conservation status but not concentrated in Europe) (Tucker & Heath, 1994). Both the skylark and song thrush are BAP species with conservation targets to be met before 2020, whilst the yellowhammer is likely to benefit from the objectives set out for the other two species.

1.9.1 *The skylark*

The skylark is the most abundant farmland bird (Poulsen et al., 1998) and is found in all types of farmland. It has a wide distribution stretching from Ireland to the Pacific, but is particularly prevalent and abundant in Europe. Declines were extensive across Europe during 1970 – 1990 (Tucker & Heath, 1994) and are still on going. In the UK alone, between 1970 and 1995 the skylark population declined by 58% (Campbell et al., 1997), despite showing only a small contraction in their range, of –1.6%, between 1970 and 1990 (Fuller et al., 1995). The start of the decline was suggested to be 1981 (Campbell et al., 1997). A UK-wide survey of skylarks in 1997 estimated there to be approximately 1 million pairs left, having decreased from 2 million pairs in 1988-91. Approximately 50% of them were on arable land (Browne et al., 2000). On lowland farmland, skylarks were recorded as declining by 58% from 1968 to 1995 (Chamberlain & Crick, 1999). Skylark population declines are not, however, restricted to farmland and declines are recorded on non-farmland habitats such as unchanged peat lands and forestry (Hancock & Avery, 1998). Nonetheless, the majority of skylarks are found on lowland farmland (Donald & Vickery, 2000), probably because farmland occupies more area than any other habitat type (Browne et al., 2000). Donald & Vickery (2000) found a positive correlation between the availability of cereals and regional skylark densities, despite the declines being steepest in regions most associated with agricultural intensification, i.e. eastern and southern Britain (Chamberlain & Crick, 1999).

Cereals are therefore an extremely important habitat to this species, covering 12.4% of total land area in the UK (Donald & Vickery, 2000).

As farmland specialists, skylarks have been affected by changes in agriculture (Fuller et al., 1995; Chamberlain & Crick, 1999; Donald, 1999). In particular, simplified crop rotations may have reduced the number of nesting attempts made per season and the switch to autumn sown cereal crops may reduce the number of suitable nesting sites as the season progresses (Wilson et al., 1997a). Loss of winter stubbles and subsequent loss of grain resources may decrease over-winter survival and fledging success may be different in set-aside than in winter cereals (Wilson et al., 1997a; Donald et al., 2002a). Despite these negative influences, skylark reproductive performance per nest showed a general improvement over time (increases in both clutch and brood sizes), which was greatest in intensively farmed habitats (Chamberlain & Crick, 1999).

Skylarks breed between April and August each year, and the male song is easily recognisable throughout the breeding season. They are one of two bird species that nest in a scrape on the ground in open fields away from tall boundary structures, the other being the lapwing. These species may therefore have benefited from the move towards larger field sizes. Skylarks can make up to 4 nest attempts a season (Snow & Perrins, 1998) and lay between 2 - 5 eggs a clutch. Both parents feed the nestlings, which are semi-precocial and leave the nest at approximately 8 days old before they can fly. Whilst adult diet is mainly granivorous, nestling diet comprises invertebrates. Little is known about fledglings once they leave the nest.

1.9.2 *The yellowhammer*

The yellowhammer is the most common, widespread bunting in the western Palearctic (Snow & Perrins, 1998), being found in open lowland and hilly countryside such as farmland, heaths and scrub. It is the last of the bunting species to go into decline and reasons for this remain largely unknown. Across Europe this species has declined by approximately 5% (Tucker & Heath, 1994), but in Britain the yellowhammer range contracted by – 8.6% from 1970 to 1990 (Fuller et al., 1995). It is reported to be Britain's fastest declining songbird, declining at a rate of 11% per year (Marchant & Wilson, 1996), with approximately 700,000 breeding pairs in the UK (Baillie et al, 2001). A recent analysis, calculating linear population changes on lowland farmland in England

and Wales, showed a continuing and rapid decline of the yellowhammer of 37.8% from 1986 – 1996 (Fuller, 2000). The decline of the British yellowhammer is unusual in that it started later than most other species, post agricultural intensification (Siriwardena et al., 1998a). This could suggest it may be able to endure agricultural intensification better than other species. The highest densities of yellowhammer actually occur in the southeast of Britain, where intensive arable production dominates (Gibbons et al., 1993).

Yellowhammer declines have, however, been longer-term in woodland habitats than on farmland (Baillie et al., 2001). This may suggest that factors driving the declines occurred in woodlands first, before they were noticeable on farmland. It has been speculated that woodlands act as a secondary habitat for yellowhammers (Baillie et al., 2001). As observed with the skylark, yellowhammer breeding performance increased during the period of declines (Siriwardena et al., 1998a; Siriwardena et al., 2000d), suggesting the decline is not related to the breeding cycle. Other studies on the ecology of the yellowhammer indicate that this species is indirectly affected by pesticide use (Morris, 2002; Boatman et al., in prep), as pesticides reduce invertebrate food supplies and affect foraging behaviour. It is likely yellowhammers suffer from loss of winter food resources. In particular increased efficiency of harvest, grain storage and loss of stubble fields, may possibly impact on winter survival.

Yellowhammers are cereal specialists, generally requiring a minimum area of cereal to maintain the population (Kyrkos et al., 1998). With polarisation across the UK, yellowhammer range contraction, from the north and west of its former range (Gibbons et al., 1993), may have been due to the lack of cereals in these areas. Yellowhammers are largely sedentary, occupying the same areas in winter as during the breeding season and 70% of winter-recovered ringed birds are within 5km of their natal territories (Lack, 1986).

British farmland yellowhammers breed between early May and August each year, generally nesting in hedgerow bases, ditches and vegetation next to ditches (Parkhurst & Lack, 1946; Stoate et al., 1998; Bradbury et al., 2000). However, males establish territories as early as February. Yellowhammers usually make up to three nest attempts a season (Snow & Perrins, 1998) and lay from 3 - 5 eggs per clutch. Both parents feed the nestlings, which leave the nest at approximately day 12. Little is known about the post-fledgling period. Whilst

adult diet is mainly granivorous, nestling diet comprises mainly invertebrates, although some grain in the diet later in the season is common (Stoate et al., 1998).

1.9.3 *The song thrush*

Song thrush distribution is widespread across Europe, with breeding occurring in most regions except those directly bordering the Mediterranean (Tucker & Heath, 1994). Northern populations move as far as North Africa or the Middle East in winter, but most populations are resident (Tucker & Heath, 1994). Song thrushes were once a common bird of woodlands, hedgerows, parks and gardens in Britain (Simms, 1978), breeding in most habitats with bushes or trees (Sharrock, 1976). Since 1962, the CBC has revealed a national decline of 73%, starting approximately in 1975 (Campbell et al., 1997). Following the harsh winter of 1962 - 63, the population fell and took three to four years to recover to a stable level before falling again in the mid - 1970s. From the period 1975 - 1993, the CBC data indicated a 65% decline in song thrushes on farmland (Fuller et al., 1995). The decline has continued (Balmer and Peach, 1996), although there is now some evidence to suggest breeding densities appears to be stabilising at this reduced level (Fuller, 2000; Baillie et al., 2001). There are now estimated to be approximately 1,100,000 breeding pairs in Britain (Gregory et al., 2002). Song thrush breeding densities are lowest on intensive arable farmland. Gardens, with their mosaic of habitats and year round food abundance, hold the majority of territories (Mason, 1998).

No published study has determined exact factors limiting the population, but an assorted array of candidate factors are implicated. Harsh winters, dry soil conditions and increased land drainage, limited food availability and pesticide use linked with agricultural intensification and predation are implicated in the declines (Davies & Snow, 1965; Baillie, 1990; Marchant et al., 1990; Campbell et al., 1997; Thomson et al., 1997; Snow & Perrins, 1998; Thomson et al., 1998; Stoate & Szczur, 2001b; Peach et al., 2004). The loss of hedgerows has also been implicated in the decline of this species (Mason, 1998), although the decline continued when the rate of hedgerow loss slowed down. There has been no reduction in reproductive performance per nesting attempt (Baillie, 1990). However, survival rates of first-year birds fell during the main period of population decline (late 1970s to 1980s) and may have been sufficient to help drive the declines (Thomson et al., 1997; Siriwardena et al., 1998a; Thomson et al., 1999). Low post-fledgling survival may have been instigated by

severe winters, although it is now thought that harsh winter weather alone could not account for the population decline (Peach et al., 2004). Hill (1998) found that the majority of song thrush fledglings died before reaching independence, a factor that may also contribute to the declines.

Song thrushes breed between March and August each year, and this long season enables them to make several nest attempts a season (Snow & Perrins, 1998). Clutch size ranges from 2 - 5 eggs per clutch. Both parents feed the nestlings, and nestlings leave the nest around day 13. Nestling diet comprises invertebrates, similar to adult diet. Post-fledging, birds are reliant on their parents for food for a further few weeks.

Appendix 1

Statistical analysis

Statistical procedures used for analysis are described in each chapter. Genstat vs 6 (Lawes Agricultural Trust, 2002), Systat vs 10 (SPSS Inc., 2000) and Excel 2000 were used for statistical analysis. Compositional analysis (Aebischer et al., 1993) is used frequently throughout the thesis so to avoid repetition is described here.

Compositional analysis was used to investigate habitat use of both breeding and foraging birds, and nestling diet, to determine which habitats/invertebrate groups were used relatively more or less than would be expected by chance. Compositional analysis was used because all analyses involved sets of proportional data. A set of components summing to one is a composition, (unit-sum constraint). Values for non-utilised but available proportions were replaced with 0.001% following (Aebischer et al., 1993), since log-ratios cannot be calculated if either proportion equals zero. Proportional habitat use and availability summed to one over all habitats and these proportions were converted to log ratio differences.

For example, if there are two habitat categories (where the sum of all proportions is equal to one) one habitat proportion is defined as the denominator ($p(d)$). It does not matter which category it is. From these two habitat categories one log ratio will be derived, calculated by $\ln(p(1)/p(d))$, to make them linearly independent. If there were seven habitat categories 6 log ratios would be derived and so on. For habitat use analysis, a single set of log-ratio differences (i.e. subtracting the 'availability' log ratios from the corresponding 'used' log ratios) were then analysed by multivariate analysis of variance (MANOVA) to test for non-random use. Wilk's lambda (value between 0 and 1) tests for significant deviance from random use, where a larger value indicates that groups are more similar. Where habitat/invertebrate use was significantly non-random, the ratio mean/standard error for each habitat/invertebrate group gives a t-value, which can be looked up on a significance table to pinpoint where non-random use occurs. From these values a matrix can be constructed ranking each habitat (or otherwise) according to relative use. Compositional analysis does not provide quantitative indices of habitat/diet use, just rankings. Each row in the table indicates the habitat used (or otherwise) as the numerator and the column habitat as the denominator. Ranks were determined by the number of positive t-values in each

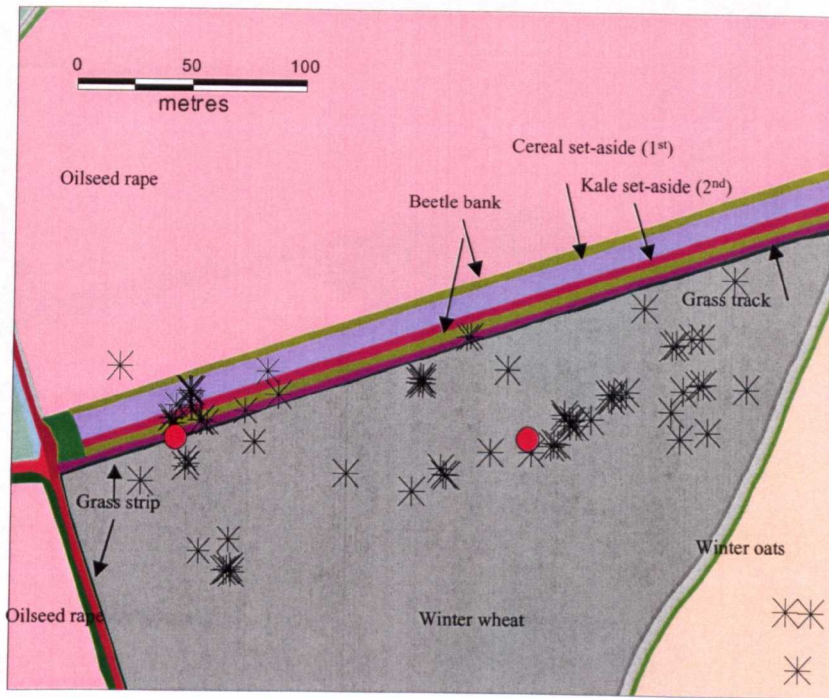
row of the matrix. The simplified ranking matrix symbol '=' means that habitats ranked the same as each other and '>' indicates that the habitat ranked higher than the following habitat type but not significantly so, '>>' significant at 0.05, '>>>' significant at 0.01, '>>>>' significant at 0.001. E.g. $a = b > c$ signifies that 'a' and habitat 'b' ranked the same as each other but higher than habitat 'c'.

However, when dealing with missing values in the 'available' habitat compositions it was not acceptable to replace them with a small value since they were not available to use. Assumptions of normality were not met. In such cases, missing values were addressed using the protocol detailed in (Aebischer et al., 1993), using the preferred method described in Appendix 2. The missing values were replaced in each column of residuals with the mean of all non-missing values for that log ratio value, because a complete matrix is required to rank habitat use. This substitution of missing values affects the independence of lambda and the random number generator in Genstat was used to produce random values (within fixed limits) that made up the matrix to produce a random value of lambda. This was repeated 1000 times to produce a series of lambda and P - values to compare with the actual calculated lambda from the data to determine the level of significance. Another method of dealing with missing available habitats is to delete the bird concerned. In the case of analysis for this thesis, this was not applicable due to small sample sizes.

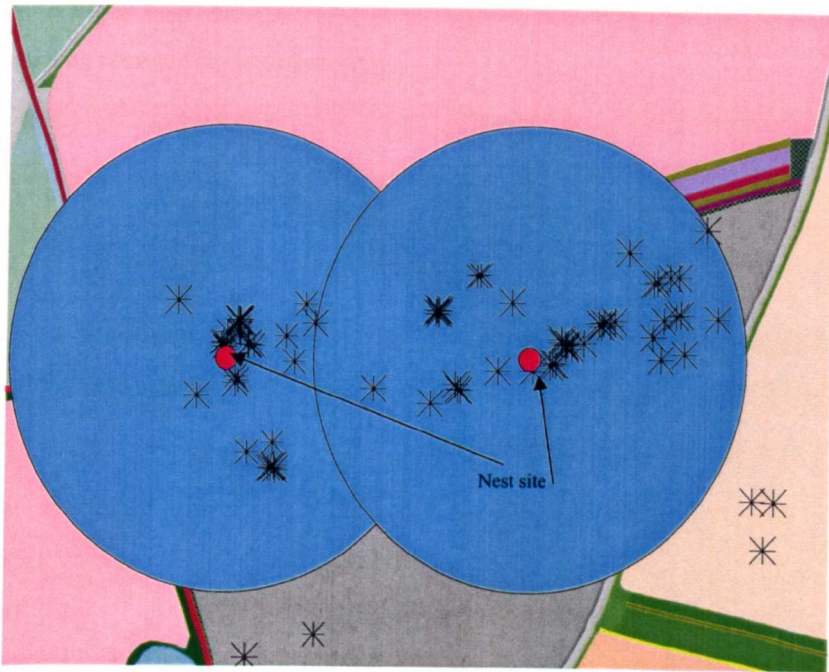
When testing for a year or species effect, paired t-tests were used to measure departure from random use once the matrix was obtained (ratio mean/standard error gives a t-value measuring departure from random use) pinpointing where non-random use occurs. Systat 10 was used for parametric statistical tests and Genstat vs 6 to program randomisation tests. Randomisation testing should be carried out when either there were missing values in the compositions for availability, or when the hypothesis of multivariate normality of the logratios was not satisfied. Bonferroni correction of significance levels was not required for reasons stated in Aebischer et al., (1993), even though repeated tests were carried out on each log-ratio.

Digital mapping

A digitised map of Loddington was made during the course of the study, using a Geographical Information System (GIS). All habitats at Loddington were featured on this map, although for the purpose of analysis some were combined. MapInfo Professional Version 7 (MapInfo, 2002) was used to calculate given areas of land, measure distances and cut out areas around nests when required for analysis and to plot triangulations.



i)



ii)

Figure a: Example maps showing skylark nest sites in one field at Loddington in 2002, one nest in a grass strip and the other in the wheat crop. i) Nests are surrounded by foraging observation points, established by direct observation of adults provisioning nestlings (crosses). Habitat types for 2002 are marked on the diagram. ii) the 95th percentile foraging distance radius around each nest (118m) was used to calculate habitat compositions around the nest (see Chapter 3). (NB: the same principles apply to the yellowhammer analysis).

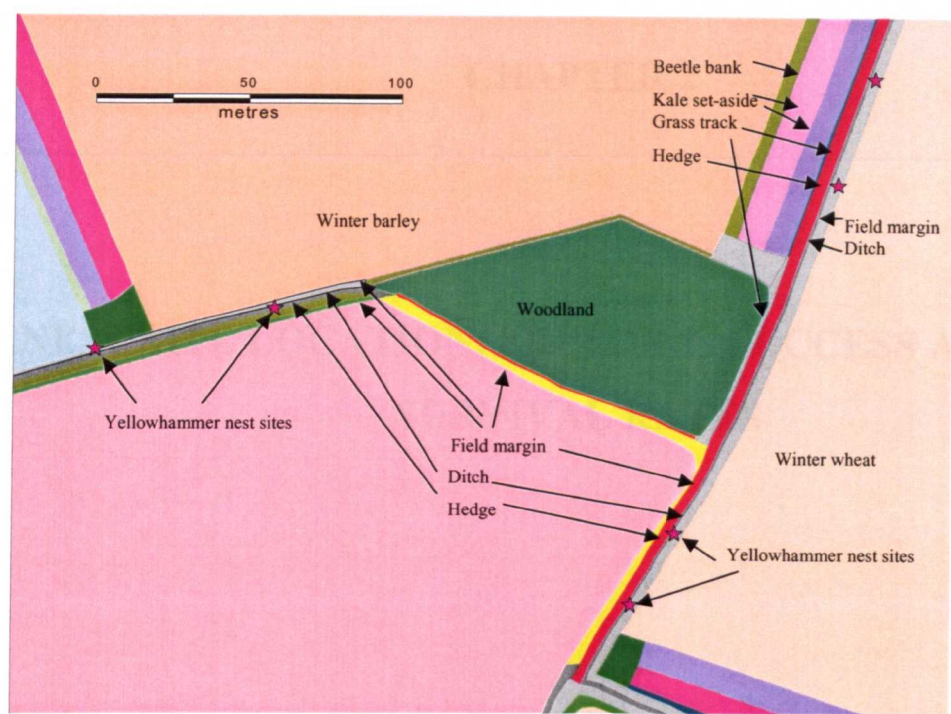


Figure b: An example map showing some yellowhammer nest sites (pink stars) at Loddington in 2000. Habitats surrounding nests are marked accordingly.

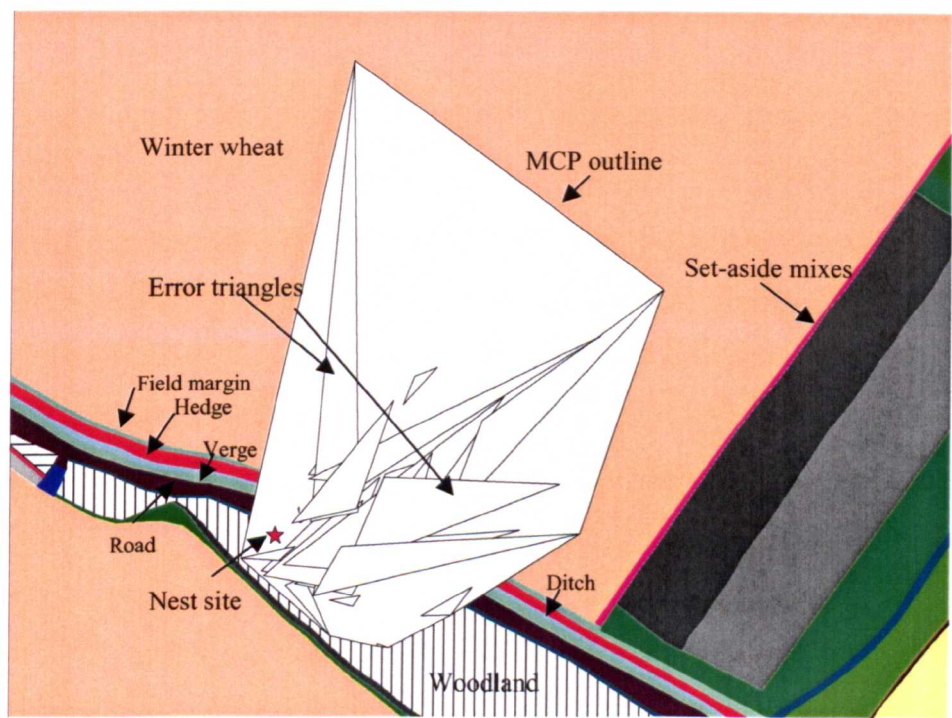


Figure c: An example map of a song thrush nest site (red star), in woodland, and the foraging minimum convex polygon (MCP) composed of foraging error triangles at Loddington (established with radio-telemetry). The various habitat types are marked on the diagram. Size of this MCP is 1.22 ha, maximum width 168m.

CHAPTER 2

NEST SITE LOCATION, BREEDING SUCCESS AND NEST SURVIVAL RATES

2.1 Summary

1. This chapter assesses nest site location, breeding success and nest survival of breeding skylarks, yellowhammers and song thrushes. This chapter specifically investigates:
 - i. Nest site location and nest density within each habitat type for breeding skylarks, yellowhammers and song thrushes.
 - ii. Whether vegetation structure or plant species composition determines nest site positioning for skylarks.
 - iii. Factors explaining variation in nest survival rates, including environmental factors, habitat composition, diet etc.
2. The greatest proportion of skylark nests were found in cereal crops and set-aside and skylark nest densities were generally highest in set-aside and lowest in crops. Yellowhammers nested exclusively in boundary habitats, such as field margins, hedgerows and ditches and other herbaceous vegetation, and nest densities were highest in field margins and herbaceous vegetation. The majority of song thrushes nested in hedgerows and woodland where nest densities were highest.
3. The vegetation structure at skylark nest sites did not differ significantly from that of control sites, either in height or vegetation density. However, skylark nest sites had significantly more grass cover present (particularly perennial grasses) than control sites and significantly less dicotyledonous cover.
4. Mean clutch sizes for skylark, yellowhammer and song thrush in this study were 3.30, 3.59 and 4.07 respectively. Mean brood sizes for skylark, yellowhammer and song thrush were 2.52, 2.61 and 2.39 and the mean number of chicks to fledge per nest attempt was 1.18, 0.84 and 1.27 respectively.
5. Over half the nests found for each species failed. The majority of nests for skylark, yellowhammer and song thrush were lost to predation (35.7%, 34.3% and 44.8% respectively of all failed nests). Most skylark and yellowhammer nests were predated in the chick stage but for the song thrush most predation occurred during the incubation period. 20% of yellowhammer broods failed due to starvation in 2000.
6. Overall nest survival rates, calculated using an extension of the Mayfield method, for the complete nesting period for skylark, yellowhammer and song thrush were 30.7%, 30.4% and 21.7% respectively.

7. Different factors affected the nest survival of each species. Skylark nest survival in the nestling stage was improved by increased vegetation density at the nest and higher chick growth rates. Increases in minimum and maximum temperatures improved yellowhammer nest survival during the incubation stage and also song thrush nest survival during the nestling stage. Increased rainfall had a negative effect on yellowhammer and song thrush nest survival during incubation. Song thrush nest survival rates during incubation were positively influenced by the area of permanent pasture around the nest and negatively so by the area of cereal. Song thrush nest survival rates during incubation also decreased when nests were built on the border of the farm and when predator control was not taking place. Song thrush nest survival during the nestling stage was affected by the month in which nestlings occupied the nest, being lower in May and August than in April and June, and by the nest site habitat, with nest survival rates being higher in woods and hedgerows than in gardens.
8. Hedgerow and field boundary management are likely to benefit nesting yellowhammers, song thrushes and other similar passerine species. Woodland management is likely to benefit nesting song thrushes and the provision of set-aside strips sown with perennial grasses is likely to benefit skylarks.

2.2 Introduction

Habitat quality is of fundamental importance to any species. Habitats provide food, shelter, breeding and over-wintering grounds, all of which can affect the demography of a species. On farmland, agricultural intensification is implicated in the serious decline of many species (e.g. Chamberlain et al., 2001a; Aebischer et al., 2000). Intensification has taken place at the expense of a number of habitats beneficial to many farmland bird species. The loss and change in structure of non-cropped habitats (such as hedgerows, grassy and herbaceous field margins), changes in cropping patterns and an increase in mechanisation and the use of chemicals, are likely to affect invertebrate food resources.

Skylarks, yellowhammers and song thrushes are all UK Red-data listed species. Their populations have declined by more than 50% since 1974 – 1999 (Gibbons et al., 1996; Gregory et al., 2002). The skylark and song thrush are also Biodiversity Action Plan species (BAP) (Anon, 1995, 1998; Gregory et al., 2002), and as a consequence are the subject of individual species plans in the UK. Skylark and song thrush populations

declined rapidly between the mid 1970s to present date, although the demise of the yellowhammer started much later than the other two species in the late 1980s. Interest in the decline of farmland birds and their conservation has prompted several studies to be carried out on the ecology of these species, with the principal aim of identifying causal factors behind their population declines at both the national and local scale (for examples see Stoate et al., 1998; Chamberlain & Crick, 1999; Donald, 1999; Gruar et al., 2003). Many of these studies suggest habitat management rationales could be met through adoption of appropriate agri-environment schemes, e.g. involving suitable woodland, hedgerow and pasture management, that could help enhance reproductive success and survival and attempt to stem the declines.

In order to establish the importance of any habitat to a particular bird species it is not sufficient to merely estimate the number of birds utilising the habitat. It must also be established how the habitat used contributes to the nest success of the species, in terms of the number of chicks that successfully fledge and which could enter the next breeding population (Newton, 1998). Nest survival is the most important factor influencing productivity at the individual scale (Martin, 1993) and nest predation is one of the main causes of nest failure of many passerine species (Ricklefs, 1969). The position of a nest can influence the likelihood of its detection by a particular predator (Bradbury et al., 2000; Stoate and Szczur, 2001a; Donald et al., 2002a) and total nest failure signifies a serious loss of reproductive effort.

Assessing nest site habitat selection is therefore essential for examining nest survival rates in relation to camouflage, predators and food abundance. Skylark, yellowhammer and song thrush are all multi-brooded, open-cup nesters and require suitable nest site habitats that offer a degree of concealment not just from potential predators, but also from the elements. Suitable nest sites must also be available across the breeding season.

The skylark is one of only two widespread lowland farmland bird species that nests solely in fields (the other being the lapwing, *Vanellus vanellus*). For skylarks, egg and chick survival in grass crops may be reduced by mechanical operations such as mowing (Schlöpfer, 1988; Wilson et al., 1997a; Poulsen et al., 1998; Donald et al., 2002a). Between 1962 - 1980 skylark clutch size and egg and chick mortalities in grassland showed very little difference to those in arable land. However, the Nest Record Card Scheme shows that about 20% more

nests in grassland survive to produce some young (O'Connor & Shrubbs, 1986). Today, silage is cut 2 -3 times in a season, which can reduce the chances of a successful first breeding attempt. Skylarks, by nesting in this habitat type later in the season (Poulsen et al., 1998), avoid disruption to breeding attempts. The number of chicks produced per hectare (i.e. breeding success) is higher on set-aside (than conventional crops) due to the increased density of breeding birds and the extended breeding season it can offer (Vickery & Buckingham, 2001). However, the review by Vickery and Buckingham highlights contrasting results reported by Donald et al. (2002a), who found nesting success of skylarks was lower on set-aside than in other crops, and Wilson et al. (1997a), who found nest survival was higher in set-aside than other crops.

Yellowhammers nest mainly in hedgerows, ditches and their herbaceous vegetation (Parkhurst & Lack, 1946; Biber, 1993b; Stoate et al., 1998; Bradbury et al., 2000; MacCleod, 2001). Song thrushes are also known to nest in hedges, woodland and gardens (Mason, 1998; Peach et al., 2004). In southern England there are hedgerows associated with no breeding song thrush territories, so hedgerow loss may not be limiting the population within its current range (Mason, 1998). This is comparable with the ciril bunting (*Emberiza cirilus*) population in south Devon where there are many hedgerows where the bunting has disappeared, (Evans, 1997). Yellowhammer and song thrush nests are susceptible to mechanical operations such as hedgerow cutting.

Decreases in nest survival rates of some species, such as the corncrake (*Crex crex*) and stone curlew (*Burhinus oedicnemus*), have been shown to drive population declines (Aebischer et al., 2000). However, these species have been shown to benefit from agri-environment schemes targeted at particular habitat creation, e.g. 'Corncrake Friendly Mowing' – mowing from the inside of the field outwards and the establishment of tilled plots for nesting for stone curlews. The study site, Loddington, introduced a suite of habitat management techniques across the farm in 1993 (see Chapter 1, section 1.6 for details, Boatman et al., 2000), including management and development of field boundaries, riparian habitats, conservation headlands and beetle banks within crops and the planting and maintenance of hedgerows and woodland. These habitats offer a range of nesting and brooding sites, refuge for over-wintering arthropods (important chick food resources), shelter and over-wintering grounds for many species. In addition to this, the farm practises crop rotation to increase habitat diversity at the field level across years.

This chapter investigates where breeding skylarks, yellowhammers and song thrushes nest at Loddington and subsequent nest survival. Although the primary focus of this chapter is on nest site habitat, other factors influencing nest survival cannot be discounted or excluded from the analysis, since the reproductive output of a pair can be influenced by other factors such as parental quality, chick food resources, environmental factors and predation. Environmental factors (primarily weather), predation and the effect of chick food availability on nest survival were also examined. Predator control took place across the farm during 2000 and 2001 (Chapter 1, section 1.6). No form of predator control took place during 2002. This chapter does not take into account the effects of pesticide application on nest survival, although it is recognised this factor can contribute to declines in some species but not others (Morris, 2002). ARET and the University of Leicester, for 2002, provided daily weather data (including minimum and maximum daily rainfall and temperatures).

The aim of this chapter was therefore to investigate (i) where skylarks, yellowhammers or song thrushes nested at Loddington and to provide estimates of nest densities within each habitat, (ii) whether vegetation structure or plant species composition determines nest site positioning for skylarks, (iii) causes of nest failure and factors explaining variation in nest survival rates.

2.3 Methodology

2.3.1 Nest finding and monitoring

Fieldwork was undertaken from the start of each species' breeding season until no further nests were found. For the song thrush this commenced in mid - March and ceased in August (2000, 2001 and 2002); for the skylark from mid - April to the end of July (2000, 2001 and 2002); and for the yellowhammer from mid-May until the end of August (2000 only).

Song thrush nests were located by cold searching all hedgerows, woodland and accessible garden areas. Skylark nests were found by observing adult birds on a daily basis for indications of breeding behaviour such as nest building, incubation and provisioning of chicks. Yellowhammer nests were also found by cold searching hedgerows, ditches and other field margin habitats. Second and third nest attempts were easier to

find once the first nest had been located within that territory. Nests were found at all stages: from initial nest building through to chicks about to fledge.

All nests were marked discreetly. In order to aid song thrush and yellowhammer nest re-location, stones, pulled up crop or grass were placed approximately 2 metres from the base of the nest. Alternatively, small pieces of coloured tape were placed in the hedge or field margin, away from the actual nest. For the skylark, white flexi-canes with red tops were used to pin point the nest site. If crop height was low (i.e. < 30cm) they were placed approximately 2 - 3 metres away from the nest, and if crop height was high (i.e. > 30cm) a small piece of coloured tape was attached to the crop near to the nest. If the nest was within set-aside or near to a track or field margin, a natural marker such as a stone or pulled up crop was used to mark the nest and a flexi-cane positioned a few metres away. These bright markers were important visual aids during skylark and yellowhammer foraging watches (see Chapter 3, section 3.3.3.1) since they enabled the observer to find the nest site quickly when a bird returned to the nest. If a bird was seen carrying nest building material the location was noted but the actual site was not visited until a couple of days later when the nest was complete, to avoid disturbing the female and the possible abandonment of her nest.

Song thrush and skylark nests were visited at least every two days and yellowhammer nests were checked every two or three days. Nests were visited with sufficient frequency to record the number of eggs and chicks, the nest outcome, chick weights and biometrics and to use neck ligatures and collect faecal sacs. Other variables collected are summarised in Table 1. Nests were monitored until either the nest failed or chicks fledged. Care was taken not to disturb the area around the nest and vegetation was rearranged to hide any path that may have attracted a predator.

Table 1: Additional nest variables collected for each species' nest attempt at Loddington. * = collected, - = not collected for that species. 'Farm centre or border' refers to whether the nest was located in the centre or border of the farm. For a nest to qualify for the centre of the farm it had to be positioned at least one field away from Loddington's boundary. A nest was considered to be on a wood margin if it was at least 3 or more metres from the wood edge.

Variable	Skylark	Yellowhammer	Song thrush
<i>Nest site habitat</i>	*	*	*
<i>Tree species</i>	-	*	*
<i>Nest height (cm)</i>	-	*	*
<i>Nearest crop</i>	*	*	*
<i>Adjacent crop</i>	*	*	*
<i>Farm centre or border</i>	*	-	*
<i>Presence and absence of a ditch or verge</i>	-	*	*
<i>Wood margin or centre</i>	-	-	*
<i>Height and width of hedge</i>	-	*	*
<i>Exposure of nest</i> (a 3-point score as in the BTO Nest Record Card Scheme)	*	*	*
<i>Height of vegetation at nest</i>	*	-	-
<i>Distance to nearest set-aside (m)</i>	*	-	-
<i>Distance to nearest hedge (m)</i>	*	-	-
<i>Distance to nearest tramline (m)</i>	*	-	-

2.3.2 Habitat structure at skylark nest sites

Vegetation cover density and botanical species percentage cover at skylark nests

These measurements were only taken for skylark. In order to minimise disturbance to the nest, once the nest attempt had finished percentage plant species cover was estimated by eye using a 0.25m² quadrat placed over each skylark nest and a single measurement of maximum vegetation height at the nest was recorded. Vertical vegetation density was measured as the percentage of a graduated 1m-'cover density' board that was covered at each of 11 height categories (H1 – H11) from a distance of two metres away and height of 1m, (0-5cm, 5-10cm, 10-20cm, 20-30cm, 30-40cm, 40-50cm, 50-60cm, 60-70cm, 70-80cm, 80-90cm, 90-100cm) (see

Chapter 2, Appendix 2, Plate 1). This was repeated four times, moving the board 90° on each occasion. A random quadrat, taken within the same habitat type at least 3 metres away, was used to take a control sample and the same measurements were collected.

2.3.3 Nest outcome and nest survival

Nests were monitored until the outcome was known. Nests were considered to be successful if at least one chick fledged. Faecal sacs around the lip of the nest and a large amount of feather scale in the nest were considered indications of successful fledging if chicks at the last check were due to fledge. For the purpose of investigating the nesting stages, the laying stage was considered to be successful if the female commenced incubation and the incubation period was deemed to be successful if one or more eggs hatched. Nests were assumed to have failed if any of the following scenarios were observed: (i) signs of predation (broken egg shells, disturbed nest, blood or chick corpses in the nest, a completely empty, intact nest containing no eggs or chicks before the expected hatch or fledge date), (ii) if the clutch was abandoned (eggs were stone cold after several visits when no adult was present) or (iii) if a whole brood was found dead in the nest (starved or chilled). Nest destruction due to agricultural operations was easily identified and only happened on one occasion (to a skylark nest). Thus nest outcome could either be categorised as success or failure. Failure could be attributed to predation, abandonment, agricultural operations, weather (e.g. chilling due to heavy rain) or starvation. While nest failure was never directly observed it was assumed to have occurred halfway between the final and penultimate nest visit (Mayfield, 1961).

For each species it was assumed eggs were laid at one-day intervals. If a nest was found in the chick stage, age was estimated using a growth curve calculated from chicks of known ages (see Chapter 5, section 5.4.4).

2.3.4 Data analysis

Analyses are based on nest data collected in 2000 - 2002 for skylark and song thrush, and 2000 for yellowhammer only. Analyses were carried out in Systat vs 10 and Genstat vs 6.

2.3.4.1 Nest site location and nest densities

Nest site location for each species was recorded and percentages of nests and nest densities per hectare (by dividing the number of nests found in each habitat by the area (per hectare) of that habitat category on the study site) for each habitat category were calculated. For skylarks 8 habitat categories (Table 2) were used in the analysis, for yellowhammers two habitat categories (Table 3) and for song thrush 6 habitat categories (Table 4).

Table 2: Skylark nest site habitat categories.

Habitat category	Habitats included
Beetle banks	Sown with a variety of grasses (see Boatman <i>et al</i> 2000) on set-aside
Broadleaved crops	Oilseed rape, winter and spring beans
Cereal	Winter wheat, winter barley, winter oats
Cereal set-aside	All years (1 st , 2 nd , 3 rd)
Grass set-aside	Including grass tracks
Kale set-aside	All years (1 st , 2 nd , 3 rd)
Other crop set-aside	Planted with crop including wild bird plots, sorghum, artichoke and partridge mixes, wildflower mixes, mustard
Other vegetation	Grass strips, non set-aside beetle banks, tall and short rough grass embankments, field margins, verge, herbaceous vegetation and short grass

Table 3: Yellowhammer nest site habitat categories.

Habitat category	Habitats included
Hedge and ditches	Hedge and ditches
Other vegetation	Grass strips, non set-aside beetle banks, tall and short rough grass embankments, field margins, verge, herbaceous vegetation and short grass

Table 4: Song thrush nest site habitat categories.

Habitat category	Habitats included
Boundary	Field margin, verge, hedge and ditch
Garden	Mown grass, gardens and grave yard
Grass vegetation	Field entrances, grass strips, short grass, tall rough grass and non set-aside beetle banks.
Herbaceous vegetation	Embankment, tall and short herbaceous vegetation, short rough vegetation
Other	Buildings, concrete, roads, stone walls, tennis courts, swimming pools, driveways, pavements, ponds and streams
Woodland	Old and new woodland

All nests found in each year were included in the analysis, regardless of whether the nest was active or not when it was found. In total, 70 skylark nests (26 in 2000, 30 in 2001 and 14 in 2002), 35 yellowhammer nests (in 2000) and 297 song thrush nests were found over the three years, (51 in 2000, 126 in 2001 and 120 in 2002).

2.3.4.2 Habitat structure at skylark nest sites

Vegetation density data were combined to produce a pooled mean for each of the 11 height categories per nest, then arcsin square root transformed to normalise data. A single mean vegetation density value was also calculated for each nest and control site, based on the individual mean values at each height interval. Vegetation height, a single measurement of the vertical structure from the centre of the nest, was recorded. Paired t-tests were used to test for differences between nest site and control site mean vegetation density and height of vegetation. Multivariate analysis of variance (MANOVA) was used to investigate differences in the height structure of vegetation at nest and control sites.

Paired t-tests were used to compare plant species percentage cover at nest sites (used) with the paired random sites within the same habitat type. Similar plant species were grouped together into the following categories: bare ground, crops (all crop types), grasses (annual and perennial), dicotyledons and other (stones, stubble, sticks etc).

2.3.4.3 Nest survival

Analysis of daily survival probabilities was made using an extension of the Mayfield method (Mayfield, 1961, 1975; Johnson, 1979), which assumes that survival rates are constant through the nesting period, based on general linear modelling (Aebischer, 1999). This method uses logistic regression to test for the effects of continuous variables and factors. The number of days on which a nest was observed (exposure days) was calculated from the day the nest was found through to the day of final nest outcome. The approach adjusts for the fact that nests are often found part way through a nesting stage, avoiding a bias towards successful nests when recording success or failure only, since successful nests are more likely to be found than early failures. A year factor was entered into the analysis for skylark and song thrush to test for a year effect. The unit of analysis was the nest and only nests that had more than one exposure day were included in the analysis. This method allows greater analytical flexibility over Mayfield methods in that continuous and categorical variables can be added singularly or in combination thus measuring their relative contribution to variation in nest survival rates. Categorical and continuous variables entered into the models are summarised in Table 5 and Table 6.

For the purpose of analysis: if the number of eggs laid, days of incubation or days to fledging were not known it was assumed for skylarks 4 eggs were laid, there were 11 days of incubation and 9 days to fledging. For yellowhammers, it was assumed 4 eggs were laid, there were 12 days of incubation and 12 days to fledge. For song thrush, it was assumed 4 eggs were laid, there were 14 days incubation and 13 days to fledge. Incubation was assumed to start on the day the last egg was laid (e.g. the 4th egg laid = day 0 of incubation). Incubation was assumed to finish on the day of hatching (i.e. 14 days incubation = hatch date = chick 0 days old).

Sample size for univariate models varied because not all nests had complete sets of data for all the variables. Using the Generalised Linear Modelling procedure in Genstat, assuming binomial errors and a logit link function, univariate models were fitted individually to examine the effects of each variable on nest survival at each stage of laying, incubation and nestling; measured according to Aebischer, (1999).

This was repeated for the whole nesting period (All), which included the total number of nest exposure days across all the nesting stages. If there were more than two significant univariate variables or factors influencing nest survival, then significant terms only were retained in the model using a forward addition approach. This allowed determination of the minimum adequate model (MAM) influencing nest survival, incorporating the number of days the nest was observed in that period as the binomial denominator. Percentage nest survival rates over the total nesting period (All) and each separate stage of the nesting period were calculated using $100[(\text{daily survival rate})^x]$, where x is the appropriate nesting period in days.

2.4 Results

2.4.1 Nest site location and nest densities

2.4.1.1 Skylarks

42.86% of all nests were found in cereal crops (31% in 2000, 37% in 2001 and 85% in 2002), 39.9% in set-aside (including habitat categories beetle bank, cereal set-aside, grass set-aside, kale set-aside and other crop set-aside; 50% in 2000, 47% in 2001 and 15% in 2002), 10% in 'other' vegetation and 7.14% in beans and (Table 7). Nest densities were generally greatest in beetle banks, cereal set-aside and grass set-aside and lowest in cereal and broadleaved crops and 'other vegetation'.

2.4.1.2 Yellowhammers

62.86% of nests were in 'Other vegetation' (i.e. habitat categories containing field margins and herbaceous vegetation) and 37.14% in hedges and ditches (Table 8). Nest densities were greatest in 'Other vegetation'. No other habitats were selected by yellowhammers for nesting at Loddington. Nest height increased throughout the breeding season ($46.86\text{cm} \pm 11.01\text{cm}$ in May to $87.5\text{cm} \pm 14.09\text{cm}$ in August) and the average height across the season was $61.00\text{cm} \pm 6.43\text{cm}$ ($n = 35$).

Table 5: Categorical variables used in the nest survival models for each species.

Species	Categorical variable	Explanation
<i>Skylarks</i>	Nest site	4-level factor of cereals, broadleaved crops, set-aside and track or verge
	Year	3 levels: 2000, 2001, 2002
	Month observed	4 levels – May, June, July and August
	Predator control	2 levels: 1 – control, 2 – no control
	Nearest and adjacent crop	3-levels: cereal, broadleaved crop, permanent pasture
	Farm centre or border	2 levels: 1 – centre or 0 - border
	Hide	3 levels of exposure (as in the BTO Nest Record Card Scheme)
<i>Yellowhammer</i>	Nest site	3-level factor of bush, herbaceous vegetation and hedge
	Month observed	4 levels – May, June, July and August
	Nearest and adjacent crop	3-levels: cereal, broadleaved crop, permanent pasture
	Farm centre or border	2 levels: 1 – centre or 0 - border
	Presence or absence of a hedge	2 levels - 0 or 1
	Presence or absence of a verge or ditch	2 levels – 1 or 2
	Hide	3 levels of exposure (the same as the BTO Nest Record Card Scheme)
<i>Song thrush</i>	Nest site	3-level factor of wood/embankment, hedge and bush, garden
	Year	3 levels: 2000, 2001, 2002
	Month observed	4 levels – May, June, July, August
	Predator control	2 levels: 1 – control, 2 – no control
	Nearest and adjacent crop	3-levels: cereal, broadleaved crop, permanent pasture
	Farm centre or border	2 levels: 1 – centre or 0 - border
	Presence or absence of a hedge	2 levels - 0 or 1
	Presence or absence of a verge or ditch	2 levels – 1 or 2
	Aspect	4 –levels (North, South, East and West)
	Hide	3 levels of exposure (the same as the BTO Nest Record Card Scheme)

Table 6: Continuous variables used in the nest survival models for skylark, yellowhammer and song thrush.

Species	Continuous variable	Explanation
<i>All species</i>	First egg date	The date the first egg was laid
<i>All species</i>	Last egg date	The date the last egg was laid, and incubation commenced.
<i>All species</i>	Hatch date	The date the eggs hatched and the nestling period commenced
<i>All species</i>	Fledge date	The date the first chick left the nest.
<i>Yellowhammer and song thrush</i>	Nest height (m)	Height of nest from the ground to the rim of the cup, log-transformed
<i>Yellowhammer and song thrush</i>	Hedge height (m)	Height of hedge from base to top, log-transformed
<i>Yellowhammer and song thrush</i>	Hedge width (m)	Log-transformed
<i>Skylark</i>	Vegetation cover density	See methods. Arcsin transformed
<i>Skylark</i>	Distance of nest from nearest hedge (m)	Log transformed
<i>Skylark</i>	Distance of nest from nearest set-aside (m)	Log-transformed
<i>All species</i>	Proportion of habitats around the nest	Determined by methods in Chapter 3
<i>Skylark</i>	Distance of nest from nearest tramline (m)	For a subset of the data only, consisting of nests in cereals only (log-transformed)
<i>All species</i>	Chick growth rate (g / day)	Determined using the difference between the first and last measurement brood mean measurements taken giving g/day weight gain (see Chapter 5)
<i>All species</i>	Five-day mean of the minimum and maximum temperatures (°C)	Prior to the period success or failure
<i>All species</i>	Five day mean of the daily amount of rainfall (mm)	Log-transformed
<i>All species</i>	Invertebrate abundance	Over-all mean abundance from invertebrate samples at known foraging sites (see Chapter 5)

Table 7: Skylark nest density per hectare at Loddington. Numbers of skylark nests found per habitat category during 2000-2002 are presented in parenthesis (n =70). Percentages of nests found over the study period in each habitat category are also presented.

Habitat category	Nest density (ha) in 2000	Nest density (ha) in 2001	Nest density (ha) in 2002	Nest density (ha) 2000-02	% of total # nests found per habitat category
Beetle bank	2.03 (2)	4.06 (4)	0.00 (0)	6.09 (6)	8.57
Broadleaved crop	0.02 (2)	0.03 (2)	0.01 (1)	0.06 (11)	7.14
Cereal crop	0.04 (8)	0.06 (11)	0.06 (11)	0.16 (30)	42.86
Cereal set-aside	1.06 (2)	0.50 (1)	0.00 (0)	1.18 (3)	5.71
Grass set-aside	0.37 (5)	0.43 (6)	0.15 (2)	0.96 (13)	15.71
Kale set-aside	0.36 (2)	0.46 (3)	0.00 (0)	0.93 (5)	7.14
Other crop set-aside	0.73 (2)	0.00 (0)	0.00 (0)	0.81 (2)	2.86
Other vegetation	0.21 (3)	0.20 (3)	0.00 (0)	0.00 (6)	10

Table 8: Yellowhammer nest density per hectare at Loddington. Numbers of yellowhammer nests found per habitat category during 2000 are presented in parenthesis (n =35). Percentages of nests found over the study period in each habitat category are also presented.

Habitat category	Nest density (ha)	% of total # nests found per habitat category
Hedges and ditches	0.14 (13)	37.14
Other vegetation	1.54 (22)	62.86

2.4.1.3 Song thrushes

The vast majority of nests were found in boundary (e.g. hedgerows) and woodland habitats (n = 276) (33.33% and 59.90% respectively) (Table 9), where nest densities were highest. Nest densities were lowest in 'other'

and gardens. There was no difference in nest height between months, but there was between years ($F_{(2, 294)} = 4.676$, $P = 0.01$). Nests were significantly higher in 2001 (mean $163.47\text{cm} \pm 6.4\text{cm}$) than 2002 (mean $140.13\text{cm} \pm 4.67\text{cm}$). The average height of song thrush nests across the study period was $151.96\text{cm} \pm 3.54\text{cm}$ ($n = 297$).

Table 9: Song thrush nest density per hectare at Loddington. Numbers of song thrush nests found per habitat category during 2000-2002 are presented in parenthesis ($n = 297$). Percentages of nests found over the study period in each habitat category are also presented.

Habitat category	Nest density (ha) in 2000	Nest density (ha) in 2001	Nest density in (ha) 2002	Nest density (ha) 2000-02	% of total # nests found per habitat category
Boundary	1.37 (23)	2.69 (45)	1.86 (31)	5.91 (99)	33.33
Garden	0.00 (0)	1.08 (4)	0.81 (3)	1.89 (7)	2.36
Herbaceous vegetation	0.23 (1)	1.25 (6)	0.69 (3)	2.24 (10)	3.37
Other	0.10 (1)	0.30 (3)	0.00 (0)	0.40 (4)	1.35
Woodland	0.90 (26)	2.37 (68)	2.89 (83)	6.16 (177)	59.60

2.4.2 Habitat structure at skylark nest sites

2.4.2.1 Vegetation density

Paired t-tests showed there was no significant difference in the mean vegetation cover density between skylark nest sites and control sites within the same habitat types, ($t = 1.39$, $P = 0.169$, $n = 69$). There was an apparent tendency for nest sites to be positioned in denser vegetation in all height categories compared to control sites (Figure 1). However, analysis of the different height categories using MANOVA, where height category was the dependent variable, also confirmed that there was no significant difference in the vegetation structure of nest and control sites, (Wilk's lambda = 0.906, $\chi^2 = 12.88$, $F = 1.19$, $P = 0.300$).

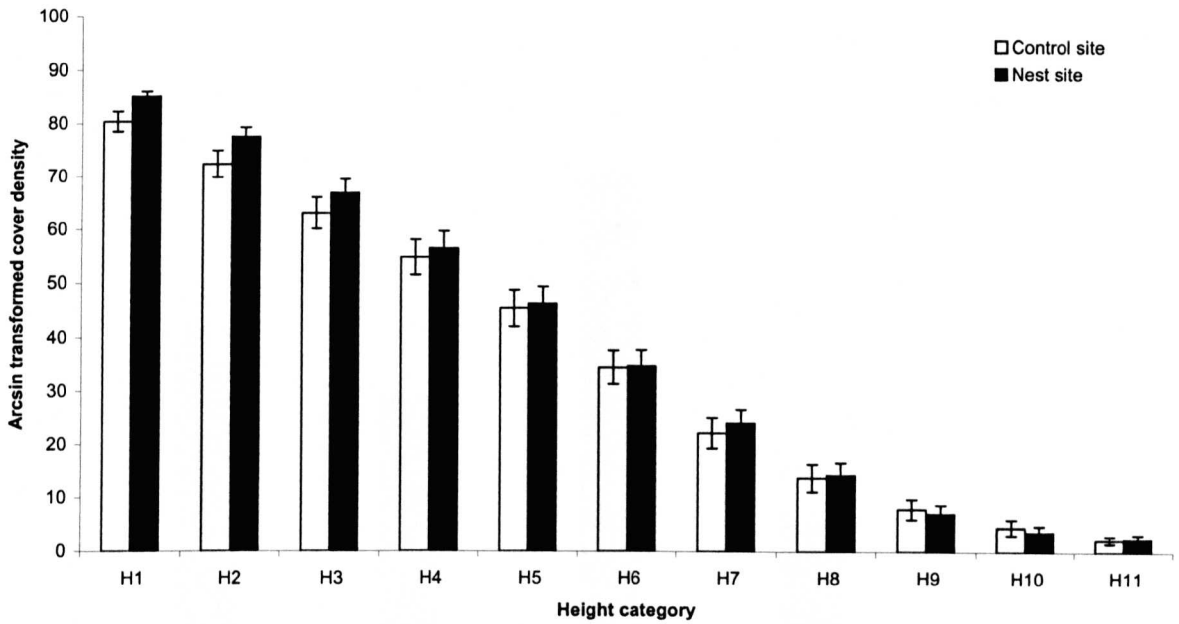


Figure 1: Mean arcsin transformed percentage cover density at each height category on the cover density board at skylark nest and control sites within the same habitat type, ± 1 SE.

Comparison of the maximum height of vegetation between nest and control sites, tested using paired t-tests, also proved not to be significant within the same habitat type ($t = 0.25$, $P = 0.803$, $n = 43$).

2.4.2.2 Plant species percentage cover at skylark nests

Separate comparisons were made between the nest and control site using paired t-tests for each plant species category, including the amount of bare ground present. Nest sites had significantly more grass cover ($t = 5.98$, $P < 0.001$) and significantly less dicotyledon cover ($t = 2.36$, $P = 0.01$) and 'other' ($t = 3.25$, $P = 0.002$) than control sites within the same habitat type (Figure 2). Grasses at both nest and control sites mainly consisted of perennial grasses (species such as cocksfoot (*Dactylis glomerata*), Yorkshire fog (*Holcus lanatus*), rye grass (*Lolium perenne*), rough meadow (*Poa trivialis*) etc), but nest sites had significantly more perennial grass cover than control sites ($t = 3.60$, $P = 0.001$).

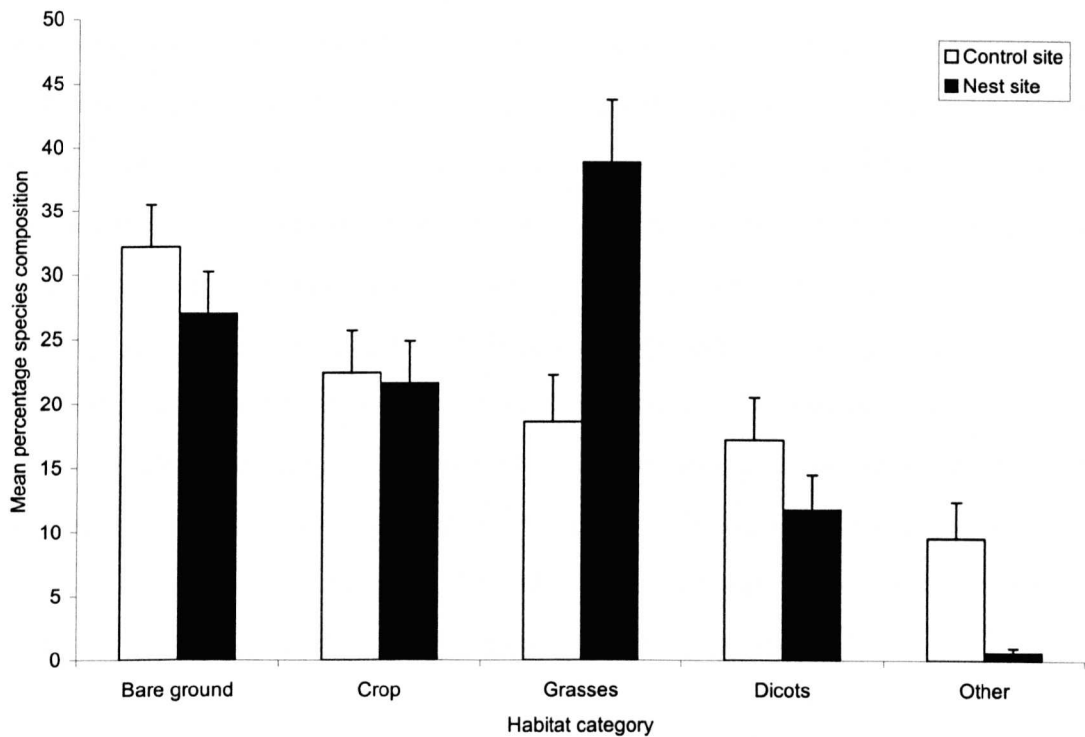


Figure 2: A comparison of the percentage plant group composition at skylark nest and control sites within the same habitat type, \pm 1SE.

2.4.3 Clutch and brood sizes

A summary of nests with known clutch size, number of eggs hatched and number of chicks that fledged is shown in Table 10.

Table 10: Mean clutch and brood size and number of fledglings produced per nest (\pm 1SE) for skylark and song thrush over the course of the study period and yellowhammer for 2000 (includes failed nests).

Species	Clutch size		Brood size		No fledged	
	Clutch size	No. nests	Brood size	No. nests	Fledging per nest	No. nests
Skylark	3.30 \pm 0.83	69	2.52 \pm 0.17	69	1.18 \pm 0.17	68
Yellowhammer	3.59 \pm 0.13	32	2.61 \pm 0.29	32	0.84 \pm 0.25	32
Song thrush	4.07 \pm 0.05	236	2.39 \pm 0.13	236	1.28 \pm 0.12	236

2.4.4 Nest outcome

Overall a high percentage of nests failed, 54.3% of skylark nests, 71.4% of yellowhammer nests and 70.7% of song thrush (from raw data). A total of 35.7%, 34.3% and 44.8% respectively of all skylark, yellowhammer and song thrush nests were lost to predation (excluding nests lost in unknown stages). For skylark and yellowhammer, most predation took place when nests had chicks, but for the song thrush it happened during the egg stage. Song thrushes appeared to abandon their nests more readily than the other two species, particularly during incubation in 2002. Poor weather conditions, such as heavy rain, snow or high temperatures, could cause birds to abandon their nests or chicks to die from starvation, so data from weather-related and starvation outcomes could be pooled with abandoned nests. 20% of all yellowhammer broods died due to starvation, which reflected the relatively few observed feeding trips made by parent birds during foraging watches (Chapter 3). Chapter 2, Appendix 2, Tables a, b and c allow a direct comparison of the percentage of nests that failed at the various stages of nesting, or that were successful.

2.4.5 Nest survival rates

Average daily survival rates for skylark and song thrush (± 1 SE) at the laying, incubation and nestling stages in 2000-2002 and for yellowhammer incubation and nestling stages are presented in Table 11. The overall survival rate for the whole of the nesting period (All) for skylark and song thrush was 30.7% and 21.7% respectively. For yellowhammers during the incubation and nestling phase (All) it was 28.9%. Song thrush nest survival was lower than both skylark and yellowhammer during the incubation stage, 52.3% compared to 71.1% and 75.7% respectively, and yellowhammer nest survival rate during the nestling period was lower than the skylark and song thrush, 38.1% compared to 50.7% and 47.9% respectively.

Table 11: Skylark, yellowhammer and song thrush daily nest survival rates (± 1 SE) for laying, incubation, nestling and 'All' stages. 'All' combines the whole nesting period.

Species	Laying	Incubation	Nestling	All
<i>Skylark</i>	0.9630 ± 0.026	0.9694 ± 0.009	0.9273 ± 0.014	0.9520 ± 0.008
<i>Yellowhammer</i>	-	0.9771 ± 0.011	0.9227 ± 0.019	0.9496 ± 0.011
<i>Song thrush</i>	0.9850 ± 0.007	0.9550 ± 0.006	0.9450 ± 0.006	0.9518 ± 0.004

The results of the univariate models show:

For *skylarks*, nest survival during the *nestling* stage was positively affected by density of vegetation at the nest site, ($\chi^2 = 4.00$, $P = 0.045$, $df = 2$, $n = 51$) and by nestling growth rate ($\chi^2 = 5.63$, $P = 0.018$, $df = 1, 24$).

For *yellowhammers*, both minimum and maximum temperatures influenced the rate of nest survival in the *incubation* stage ($\chi^2 = 6.16$, $P = 0.013$ and $\chi^2 = 5.59$, $P = 0.018$, $df = 1$, $n = 21$). As minimum and maximum daily temperatures increased so did egg survival rates. The amount of rainfall negatively influenced nest survival during incubation ($\chi^2 = 10.26$, $P = 0.001$, $df = 1$, $n = 23$). There were no significant effects during the nestling stage.

For *song thrushes* (see Table 12) nest survival rates during the *laying* stage were negatively influenced by the amount of rainfall ($\chi^2 = 4.06$, $P = 0.044$, $df = 1$, $n = 82$).

During *incubation* nest survival rates were influenced by predator control ($\chi^2 = 3.97$, $P = 0.046$, $df = 1$, 185), nests having more chance of survival when predator control was taking place (0.957 ± 0.006) than when it was not (0.932 ± 0.012). Whether the nest was situated in the centre of the farm ($\chi^2 = 12.29$, $P < 0.001$, $df = 1$, 185) also influenced nest survival and nests were more likely to survive in the centre of the farm (0.967 ± 0.006) than the border (0.920 ± 0.011). The proportion of permanent pasture and cereal around the nest affected survival rates during incubation (permanent pasture; $\chi^2 = 4.11$, $P < 0.043$, $df = 1, 185$; cereal; $\chi^2 = 3.99$, $P = 0.046$, $df = 1, 185$). Nest survival rates improved with increasing proportions of permanent pasture (0.9681 ± 0.009) and decreasing proportions of cereal crops around the nest (0.962 ± 0.007).

During the *nestling* stage, the month in which chicks were in the nest influenced nest survival ($\chi^2 = 4.54$, $P < 0.001$, $df = 4$, $n = 145$). Chicks were more likely to survive in June (0.970 ± 0.01) and July (0.970 ± 0.011) but had a lower chance of survival in April (0.933 ± 0.012), May (0.936 ± 0.014) and August (0.500 ± 0.204). Nest site habitat affected nestling survival ($\chi^2 = 3.53$, $P = 0.029$, $df = 2$, $n = 145$). Nestlings in gardens had less chance of survival (0.792 ± 0.09) than those situated in woods (0.950 ± 0.008) or hedges (0.949 ± 0.01). Minimum and maximum temperatures also positively influenced nest survival at the nestling stage ($\chi^2 = 4.81$, $P = 0.028$ and $\chi^2 = 4.87$, $P = 0.030$, $df = 1$, $n = 140$).

Across all nest stages, song thrush (*All*) nest survival was affected by year ($\chi^2 = 4.177$, $P = 0.015$, $df = 1$, 222, 2000 – 0.966 ± 0.07 , 2001 – 0.954 ± 0.006 , 2002 – 0.936 ± 0.008). Analysis showed daily nest survival rates were lowest when there was no predator control in 2002 (0.937 ± 0.006) than when predator control was taking place in 2000 and 2001 ($\chi^2 = 6.63$, $P = 0.010$, $df = 1$, 222, 0.960 ± 0.004). Nest survival was affected by whether the nest was situated near the farm centre or border ($\chi^2 = 8.747$, $P = 0.003$, $df = 1$, 222), having higher survival rates in the farm centre (0.961 ± 0.004) than the border (0.937 ± 0.007). The date incubation started also affected the total nest survival ($\chi^2 = 6.78$, $P = 0.009$, $df = 1$, 180) with nest survival being higher early in the season (0.9745 ± 0.005) compared to later in the season (0.945 ± 0.009).

No other recorded variables influenced nest survival and there were no significant effects of year at any nesting stage for any species. None of the variables tested significantly affected nest survival rates for either the skylark or yellowhammer across the complete nesting period (*All*).

Table 12: Univariate variables that significantly affected song thrush nest survival at the various stages. * = significance at $P < 0.05$, ** < 0.01 , *** < 0.001 .

Nesting stage	Variable	Effect on nest survival	Univariate significance
<i>Laying</i>	Rainfall	- ve	*
<i>Incubation</i>	Predator control		*
	Farm centre / border		***
	Proportion permanent pasture	+ve	*
	Proportion cereal	-ve	*
<i>Nestling</i>	Month		***
	Habitat		*
	Temperature	+ve	*
<i>'All'</i>	Year		*
	Predator control		**
	Date incubation started		**

The results of the *multivariate* models show:

For *skylarks* the best minimum adequate model (MAM) explaining nest survival during the *nestling* stage only included growth rate ($\chi^2 = 5.63$, $P = 0.018$, $df = 1,24$). Adding the variable 'cover density at the nest' did not produce any significant change in deviance.

For *yellowhammers* the best MAM included rainfall during *incubation* ($\chi^2 = 10.26$, $P = 0.001$, $df = 1$). Adding the minimum, maximum or mean temperatures did not produce any significant changes in deviance.

For *song thrushes* during the *incubation stage*, the best-fit model explaining nest survival included farm 'centre' or 'border' and the proportion of permanent pasture around the nest ($\chi^2 = 8.60$, $P < 0.001$, $df = 2$). There was a significant interaction between the two variables, $\chi^2 = 5.89$, $P < 0.001$, $df = 3$.

During the song thrush *nestling stage* the best model explaining nest survival was 'month' and 'habitat' ($\chi^2 = 4.05$, $P = 0.017$, $df = 2$). Thus the effects on nest survival at the nestling stage of month and habitat type were significant in their own right. There was a significant interaction between the month young were in the nest and the habitat type the nest was in ($\chi^2 = 3.35$, $P < 0.001$, $df = 1$), which may reflect a change in nest site over the breeding season that would affect survival.

The best MAM to explain the '*All*' nest survival for the song thrush included the 'farm centre or border' factor + date of last egg laid ($\chi^2 = 7.64$, $P < 0.001$, $df = 180$).

2.5 Discussion

2.5.1 Nest site location and suitability

2.5.1.1 Skylarks

At Loddington, set-aside supported a large proportion of skylark nests found and nest density was generally greater there than in cereal crops, despite cereals also holding a large proportion of nests over the study period. The close association of set-aside with nesting skylarks at this site has previously been recorded by Boatman & Bence (2000). Set-aside provides a heterogeneous habitat suitable for nesting across the entire breeding season (Vickery & Buckingham, 2001; Eraud & Boutin, 2002). Set-aside sown in strips, at Loddington, is mainly non-rotational and it provides a mix of sward structures and bare patches across the breeding season from newly sown strips to established strips, for example cereal, kale, wildflower or grass mixes. These strips not only provide a good source of cover for nests but also increase insect abundance, important chick food sources (Poulsen, 1996). The abundance of skylarks has been reported as being highest on rotational set-aside in other studies, (e.g, Henderson & Evans, 2000) and lowest on winter cereals as the breeding season progresses (Schläpfer, 1988; Wilson et al., 1997a; Chamberlain et al., 1999a; Donald & Vickery, 2000; Eraud & Boutin, 2002).

Patchy vegetation at the nest site may help camouflage the nest and the diverse sward structure within set-aside may facilitate this. Skylark preference for set-aside during the breeding season has been highlighted by a number of studies (Wilson et al., 1997a; Poulsen et al., 1998; Chamberlain & Crick, 1999; Donald et al., 2001b), but none of these studies examined set-aside managed for gamebirds and other wildlife. Winter cereals appeared to hold lower nest densities than set-aside at Loddington, which may reflect the crop structure as suggested by Wilson et al. (1997a), although it was still used as a nesting habitat later on in the season in the current study. Skylark population densities (recorded as the number of singing males) decrease in winter cereals as the breeding season progresses, but increase in spring cereals due to more open vegetation structure in the latter (Schläpfer, 1988; Wilson et al., 1997a; Chamberlain et al., 1999a). Chamberlain et al. (1999a) found the greatest skylark occupancy in arable landscapes in vegetation under 30cm. However, at Loddington

all cereals grown were winter varieties so inevitably were approximately 30cm tall at the start of the breeding seasons. Skylarks nesting in them could have been selecting a microhabitat suitable for nesting.

However, within nesting habitats, skylarks did not appear to be selecting areas with specific vegetation heights or vegetation density. This could be due to the sampling technique used in the study (with measurements taken at the end of the attempt rather than the start when birds were choosing nest sites). If the control quadrat had been taken much further away from the nest, one may have also expected to find more obvious differences. However, skylark nest sites contained more grasses, particularly perennial grass species such as cocksfoot, Yorkshire fog, rye grass and rough meadow, than surrounding areas within the same habitat type. These grasses may have provided structural support to both the nest and tunnels leading into them, which became more pronounced with increased use. Since these perennial grasses are relatively strong and sturdy they are less likely to be flattened by the constant coming and going of adult birds. They may shield the nest to some degree from predators. Nests are usually built within supportive stems, which may be the reason why there was significantly less dicotyledonous cover present at nest sites. Although it is widely accepted that winter cereals become less attractive as potential skylark nesting sites (Wilson et al., 1997a; Chamberlain et al., 1999a), due to both the height and dense ground cover, the study at Loddington found that, as the crop ripened, foliage became less dense and more bare ground was exposed (pers. obs). This may have been a reason why skylarks still utilised winter cereals towards the end of the breeding season, particularly if, in contrast, set-aside became denser, which occurred on some set-aside strips.

Other studies have examined the suitability of crops for nesting at the field level by taking a series of height measurements across the field rather than directly at nest sites (e.g. Wilson et al., 1997a; Chamberlain et al., 1999a) and over the course of a breeding season. Their results show that vegetation height within different habitat types does influence nest site selection by skylarks in arable habitats. In the current study, maximum vegetation height at the nest was recorded at the end of each nest attempt in an effort to standardise measurements, since not all nests were found in the same stage of the nest cycle, and to minimise disturbance to the nest. Wilson et al. (1997a) and Chamberlain et al. (1999a) found that crop suitability for skylark nesting was around 20 - 60cm. The Loddington study found that overall mean maximum vegetation height at the skylark nest site was $61.45\text{cm} \pm 26.50$ (minimum height 8cm, maximum height 110cm, $n = 64$). This is at the upper end of the suggested optimal vegetation heights suggested previously, but much taller than that reported

by Jenny (1990b) and Schläpfer (1988) in Switzerland, although Jenny also reports nests being found in crops of 60 - 100cm. Skylarks could be selecting specific areas within crops of optimum heights (established by the above studies), but at higher vegetation heights than expected within them, to offer the nest a degree of protection from avian predators. The creation of sparse cereal sward or even bare ground within cereal fields (Odderskaer et al., 1997), may enhance nest site availability for skylarks, but how the microhabitat at the nest site provides cues to the birds as to where to place their nests is largely unknown. A study carried out by the RSPB to improve the suitability of winter wheat for skylark nest sites, left large bare patches within the crop to see whether skylarks used them in preference to the crop. Preliminary results suggest that these plots (created by turning off the drill) may help to lengthen the breeding season by providing both nesting and feeding sites (Morris et al., 2003).

In the third year of the study it was surprising to find only 2 nests in set-aside, one in a grass track and one on a grass verge, with the rest being situated in crops (11 in winter cereals and 1 in beans). During this year male skylarks stopped advertising their territories during mid-June and it became difficult to find nests, if the birds were indeed still breeding. Crops in this year appeared to be more uniform in structure and stem density than in previous years, with fewer sparse patches created either through heavy rain early in the year, or damage from pests such as woodpigeons (*Columba palumbus*) or hares (*Lepus capensis*). Set-aside was also generally thicker (pers. obs), being sown with more cereal-based mixes than before. This may have made it more unattractive to nesting skylarks as the season progressed. In contrast, skylark activity persisted through to the end of the breeding season on farmland adjacent to Loddington. So, despite the diverse habitats available to skylarks at Loddington (Boatman et al., 2000) it is possible that habitats within territories became unsuitable for nesting due to changes in vegetation structure. These possible changes could have resulted in a spatial shift in territories or early curtailment of breeding activity. Schläpfer (1988), Jenny (1990a), Wilson et al. (1997a) and Donald et al. (2001b) also suggest that low habitat diversity and inappropriate vegetation structure within a territory could cause a shift in territory or the cessation of the breeding season.

Bean and oilseed rape crops were not commonly used to nest in. This is most likely to be due to the fast-growing nature of the crops. Bean fields were only used very early on in the season when the crop was low and there was a lot of bare ground between plants. No skylark nest was ever found in oilseed rape despite a

couple of birds holding territories over them. Recent increased rape area may prove detrimental to breeding skylarks, reducing the available nesting habitat to them further and possibly reducing the number of nest attempts per pair. Wilson et al. (1997a) found no breeding attempts in legume or oilseed rape fields despite territories being present. From 2002, Loddington ceased growing winter barley and substituted this with oats. Winter oat crops tend to be fast growing and dense, possibly making the cropped area unattractive to nesting birds earlier in the season than winter barley.

2.5.1.2 Yellowhammers

As with other studies (Parkhurst & Lack, 1946; Peakall, 1960; Stoate et al., 1998; Bradbury et al., 2000; Bradbury & Stoate, 2000; MacCleod, 2001) the current study found that yellowhammers consistently nested in hedgerows, ditches and herbaceous vegetation along these habitats, although MacCleod (2001) also found them in conifer trees. These habitats may offer a good degree of concealment from avian predators, whilst providing invertebrates suitable for chick food (Dennis et al., 1994). Nest survival was fairly consistent between bushes (0.9424 ± 0.012), herbaceous vegetation at the base of ditches and hedges (0.9561 ± 0.191) and in the hedgerow itself (0.9514 ± 0.018).

Approximately half of Britain's hedgerows were lost between 1947 and 1990 (Barr & Parr, 1996). Since yellowhammers are hedgerow specialists preferring non-roadside hedges to roadside hedges (Fuller et al., 2001), this could have affected national breeding populations. At Loddington, the hedgerow and field boundary management taking place is likely to benefit the local population. Decreases in the population are more likely to be caused by other factors affecting nest survival such as predation or availability of food sources (although not proved in this study). Nest height increased throughout the season, consistent with Parkhurst & Lack (1946), Stoate et al. (1998), Bradbury & Stoate (2000), Stoate & Szczur (2001a) and MacCleod (2001), although in this study and MacCleod (2001) the increase was not significant.

2.5.1.3 Song thrushes

Song thrushes are associated with woodland or woodland edges (Chamberlain & Fuller, 1999) and at Loddington they nested mainly in woodland and hedgerows, where nest densities were highest. As with the yellowhammer, it is likely that hedgerow and woodland management at Loddington benefits this species with regard to nest sites. However, song thrushes were not found to be either hedgerow or woodland specialists in the study conducted by Fuller et al. (2001) using British Trust of Ornithology (BTO) data from the Common Birds Census (CBC). Nest densities were low in gardens at Loddington, although this result may be an underestimation since not all gardens could be checked for nests. Although gardens formed a small habitat area across the study site they comprised many singing male territories (unpublished data). Nest survival was low in gardens, which may reflect cat predation or interference from humans.

Many hedgerows at Loddington were severely cut back at the start of the 2002-breeding season after remaining uncut for approximately 4 years, which may explain the significant difference in average song thrush nest heights between years. The lack of hedgerow cover at the start of the 2002 - breeding season appeared to attract fewer birds to nest there. Lack (1987) showed that severe hedge cutting could seriously reduce the territory numbers of many bird species that utilise those hedgerows. Mason (1998) found that song thrushes in Cambridgeshire were associated with hedgerows of 4 - 5 metres in height, while most of the hedgerows at Loddington approached heights of 3 - 4m. Hedgerow and woodland vegetation structure offer a good degree of concealment from nest predators. In contrast to the results of this study, Schnäck (1991) found song thrush nest height increased over the course of the breeding season in Vienna and found the majority of nests were between 2 – 3.5m high. 80% of Schnäck's nests were built in conifers in April, but changed to deciduous trees and shrubs later in the season. At Loddington, song thrushes also often nested in conifers, but this was not restricted to the start of the breeding season since many of the young woodland plantations were planted with spruce trees. Drycz (1969) and Bocheński (1968) also report conifers as a most used nest site.

2.5.2 Causes of nest failure

The majority of nests for each species failed, and the main cause of failure was due to predation, as might be expected (Ricklefs, 1969).

2.5.2.1 Skylarks

On farmland, Wilson et al. (1997a), Weibel (1999) and Donald et al. (2002a) also report that predation is the main cause of skylark nest failures (50%, 72% and 77% of all nests found respectively). Nest losses due to predation were lower in this study (35.7%) and this could be due to the predator control in the first two years of the study. Evidence to show that predator control can significantly benefit skylark nest survival rates is shown by Donald et al. (2002a) who, following the initiation of intensive predator control at one of his study sites, reported that nest survival rates significantly increased from 12.3% to 40.7% (when many other factors were held constant). In the current study, predation occurred more in the nestling stage than in the egg stage, as was found by Weibel (1999). Delius (1965) on his sand dune population in northwest England also found that predation was the main cause of nest failure.

At Loddington it was often difficult to determine the nest predator precisely. Nests that had been completely destroyed were thought to have been so by mammalian predators, which are likely to detect nests from olfactory cues. Avian predators are reliant on visual cues and were thought to be responsible if nests were found completely empty but intact. Sparrowhawks (*Accipiter nisus*) would occasionally be responsible for adult predation and on more than one occasion the female was found decapitated near the nest. If several nests were in one habitat type it is likely that predators were able to detect them one after the other, which means they would not be independent from one another.

Skylarks nest in open fields, which makes them more vulnerable to agricultural operations. Losses due to agriculture were uncommon in this study with only one skylark nest being destroyed due to agricultural operations. However, other studies where skylarks have nested in grass crops have reported mowing as a main cause of failure (Schlöpfer, 1988; Jenny, 1990a; Poulsen et al., 1998; Donald et al., 2002a).

Wilson et al. (1997a) and Poulsen et al. (1998) reported all cases of skylark brood starvation in cereal fields (14%). In the current study, although it was the third most common cause of nest failure, alongside adverse weather conditions, it happened infrequently and was not exclusive to cereal fields (5.71%), also occurring in legumes but not in set-aside.

2.5.2.2 Yellowhammers

Predation was the main cause of nest failure in this study. Most predated nests were lost during the nestling stage, as found by Crick et al. (1994), in their study of 4 bunting species from BTO nest record cards, and Bradbury et al. (2000). At Loddington this could be attributed to the high level of starvation, which could increase begging rates and thereby attract predators, as suggested by Evans et al. (1997) with ciril bunting chicks. There appeared to be no difference in survival rates in the different nesting habitats although Stoate & Szczur (2001a) found that nests with young had significantly higher survival rates in herbaceous vegetation than in hedges at the same study site between 1995 - 98. The authors suggested that this could be attributed to nest concealment from predators, different predation pressures in the two habitat types or to density dependent effects resulting from the larger number of passerine species nesting in hedges.

In this study, yellowhammer nests were generally immune to mechanical losses, most likely because hedgerows at Loddington were trimmed outside the breeding season and the herbaceous vegetation bordering hedgerows was not cut. Mechanical operations on surrounding farms were known to cause the failure of both passerine and gamebird nests towards the end of the season (Szczur pers. comm). Crick et al. (1994) found that agricultural operations were more likely to destroy yellowhammer nest attempts during the incubation stage than the chick stage, which remained about the same pre and post 1970.

As with skylarks, predators of yellowhammer nests often left no visual clues as to their type. Therefore, determining the exact nest predator was not always possible. Nests were frequently left perfectly intact with no signs of predation, which may be indicative of an avian predator. Mammalian predators, which find nests mainly through olfactory cues, more often than not damaged the nest. Mice (*Apodemus sylvaticus*, *Mus*

musculus) ate through the eggs leaving partially eaten or broken eggshells. Snakes left holes through the bottom of the nest and one was seen curled on top of a nest (Szczur pers. comm).

2.5.2.3 Song thrushes

Out of the three study species, the song thrush experienced the highest proportion of nest failure due to predation. Predation occurred more frequently in the egg stage than the chick stage, supporting findings by Silva (1949), Snow (1955), Drycz (1969) and Götmark et al. (1995). It has been hypothesised that the bright blue egg colouration of the song thrush may attract the attention of predators, but a study by Götmark (1992) using artificial eggs found that predators spot the nest before the eggs. Corvids are most likely to be the main predators of song thrush nests (Götmark, 1992), although evidence of mice, grass snakes (*Natrix natrix*) and larger mammals was also observed in this study. Song thrushes are particularly obvious when entering and leaving the nest site, making them vulnerable to visual predators. Sparrowhawks are predators of song thrush adults, nestlings and fledglings (Götmark et al., 1995– unpublished data). Two radio-tagged adults (see Chapter 3) and several colour-ringed nestlings and fledglings were found under a sparrowhawk nest in 2002 at Loddington. The second largest cause of nest failure was abandonment. This also generally occurred in the egg stage, particularly during adverse weather conditions. Such ‘abandonment’ could be attributed to predation of adults in some cases.

2.5.3 Clutch and brood sizes

2.5.3.1 Skylarks

Clutch size and brood size are widely documented for this species (see Delius 1965; O'Connor & Shrubbs, 1986; Schläpfer, 1988; Jenny, 1990a; Wilson et al., 1997a; Poulsen et al., 1998; Chamberlain & Crick, 1999; Weibel, 1999; Donald et al., 2001e). Clutch size in this study was between 2 - 4 eggs per clutch. No clutches of five were recorded as in many of the above studies. The mean clutch size, 3.30 ± 0.83 , in this study was lower than most of the other studies and all but one clutch hatched synchronously, when 2 eggs hatched on consecutive days, 2 days after the first to hatch. The late hatchlings subsequently died. Poulsen et al. (1998)

also reported asynchronous hatching although this is unusual (Cramp, 1988). Clutch size also increased over the season, as described in Schläpfer (1988) and Jenny (1990a), and declined in July the final month of laying, the same as in Weibel (1999).

The mean number of chicks that fledged per nest attempt was also lower than in other studies, which is cause for concern when considering the reproductive performance of the species with regard to population declines. However, as many of the studies do not find all nests, start at different times in the season and estimate number of fledglings differently, meaningful comparisons between studies are difficult to make. Availability of suitable chick food could cause the differences in the number of chicks fledged, although most territories at Loddington were associated with set-aside, which is known for its abundant chick food resources. Chamberlain & Crick (1999) reported a linear increase in skylark clutch and brood size between 1950 and 1994, when they investigated changes in reproductive performance of CBC and Nest Record Card Scheme (NRCS) data at the BTO. They found an improvement in reproductive performance over this time period, with the greatest improvement on intensively farmed agricultural habitats.

The overall nest survival rate of the Loddington skylark population, 30.7%, is slightly higher than the 24.2% reported by Donald et al. (2002a) in lowland agricultural habitats in southern England, or 27% by Chamberlain & Crick (1999) in agricultural habitats between 1975 – 1994 in the UK. Differences could be due to localities, time periods in which they were studied or sample size. A maximum of 4 nest attempts per pair was estimated to have taken place over the current study period. However, because birds were not individually marked, there has to be a degree of uncertainty in this statement. Jenny (1990a) found at his study site in Switzerland that skylarks made a maximum of 6 nesting attempts while Wilson et al. (1997a) suggest pairs need to make 2 - 3 nesting attempts per season to sustain the population. From 1992 – 2001 the skylark population at Loddington has remained stable (Stoate and Leake, 2002). Perhaps this observed level of productivity is just sufficient to maintain, but not increase, the current population level, even if immigration and emigration were taken into account.

2.5.3.2 Yellowhammers

Clutch size during 2000 was similar to that found by Stoate et al. (1998), Yomtov (1992) and Bradbury et al. (2000). The number of young fledged per successful nest (2.5 ± 0.35) was similar to that reported by Bradbury et al. (2000) of 2.6 ± 0.06 . However, in the current study the overall mean number of fledglings produced per nest (including nest failures) was disturbingly low (0.84 fledgling per nesting attempt), particularly in comparison with results from the same site in 1992 and 1993 of 2.72 ± 0.19 and 2.62 ± 0.22 fledglings per nest respectively (Stoate et al., 1998). In the current study there was no attempt to find and monitor all nests across the whole breeding season so comparisons should be made with caution. Low fledging rate could have been specific to those nests found or to environmental conditions that season. Indeed, in 1995 at Loddington, Stoate et al. (1998) also recorded a low number of fledglings per nest (0.95 ± 0.27) and related it to the cold weather and the fact that they only monitored first broods. The estimated 0.77 fledglings per nesting attempt in the current study are too low for the population at Loddington to maintain stability. In conjunction with low fledgling success there has been a decrease in the number of yellowhammer territories held at Loddington in recent years (Chris Stoate, pers.comm). This contributed to the decision to stop the current study after only one season, in case low nest survival was, in part, due to the monitoring itself.

2.5.3.3 Song thrushes

Most eggs hatched over a 24 - hour period although some nests did hatch the last egg a day later. Hartley (1967) concluded that eggs hatched over a 2 - day period during the summer and Lack (1966) also reported that large clutches may not hatch together for the similar species, blackbird (*Turdus merula*). Baillie (1990), using BTO national data, found that the average clutch size of song thrush (4.1) has been constant through time. The current study's average clutch size of 4.07 is similar to that of previous studies within the UK and other European countries (e.g. Silva, 1949; Snow, 1955; Pikula, 1969; Thomson & Cotton, 2000) and consisted of between 2 –5 eggs. Baillie (1990) also found that hatching success and fledging success increased slightly over their study period between 1962-1981. His estimated egg survival rates were higher than found in this study, but his daily survival rates for chicks were lower.

Baillie's work (1990) suggested that the population decline of the song thrush was not being driven by reduced individual reproductive performance or adult annual survival rates (except during the cold winter of 1962/63). It was more likely to be due to a decline in post-fledgling survival rates (Thomson & Cotton, 2000), which was beyond the scope of this project to examine, or the number of breeding attempts made per individual. The current study estimated that up to 5 nesting attempts were made by song thrush pairs at Loddington, which is higher than the number recorded (up to 4) by Thomson & Cotton (2000) in their 'stable study site' in Sussex. Song thrush densities have increased by over 400% since 1992 at Loddington and as a result the population may now be at carrying capacity. Certain habitats may now be saturated and this can be seen by the close proximity of some breeding females, sometimes nesting less than 15m apart. Thomson and Cotton (2000) recorded a mean 3.3 fledglings from successful nests. The current study had a higher fledging rate per successful nest of 3.73. Since Loddington has been so successful in increasing the song thrush breeding population, it is a possibility that Loddington could act as a source population for nearby sites. It could be possible that the similarity in reproductive rates at Loddington with other studies, despite the high breeding densities, may provide indirect evidence that the cause of the song thrush decline lies elsewhere in the life cycle.

2.5.4 Factors affecting nest survival rates

2.5.4.1 Skylarks

Results from this study showed that the two main factors which independently and positively influenced skylark nestling survival rates were the amount of vegetation cover density at the nest site and chick growth rates. Increasing vegetation density at the nest site was likely to serve as concealment from avian rather than mammalian predators. Growth rates were likely to be affected by diet, foraging habitats around the nest (examined later in the thesis) together with parental quality and experience.

Donald et al. (2002a) found that the crop type in which the nest was located, the intensity of predator control and annual effects, such as weather, influenced nest survival. The current study did not find that these factors influenced nest survival but both studies found the significant variables appeared to have an effect at the chick

stage only, perhaps reflecting the fact that adult birds were more active once chicks were in the nest. Nest survival in winter cereals was found to be double that in set-aside or agricultural grassland by Donald et al. (2002a), supported by Jenny (1990a) and Weibel (1999), although Wilson et al. (1997a) found nests survived better in set-aside than winter cereals. The results from the current study concurred with Wilson et al. (1997a) and found that nest survival rates were higher in set-aside (0.9613 ± 0.016 , i.e. 42% compared to Donald's 21.8% and Wilson's similar 44%) than winter cereals (0.9509 ± 0.014 , i.e. 33% compared to Donald's 38% and Wilson's much lower 11%). The Loddington study did not support Donald et al. (2002a) who found that survival of nests in cereals was affected by how close they were to tramlines, although sample sizes were much smaller.

Chick growth rates also affected nest survival rates in the current study and this may be partly explained by increased chick food availability within set-aside or by better concealment from predators. Although Chamberlain et al. (1999a) suggest that crop structure is more important than food availability, it cannot be ruled out that both could have an effect on nest survival rates. Results in Chapter 5 on chick growth rates show that the proportion of set-aside around the nest, which in turn has been shown to increase nest survival here, is positively correlated with skylark chick growth rates. Nevertheless, habitat composition surrounding successful and unsuccessful nests in this study did not differ between nests that hatched young and fledged young and those that hatched young and failed to fledge. Sample size in this study was small compared to Donald et al. (2002a), where almost 1000 nests were used in the analysis. This may account for the discrepancies, or the result may be attributed to the localities.

No other variables tested significantly affected skylark nest survival rates although one may have expected the distance from boundary features, such as hedgerows or the proportion of woodland, around the nest to have done so. As these habitats are likely to hold predators, skylark nests closer to them may experience an increased risk from predation. The effect of the removal of predator control from Loddington was not apparent. However it is likely in future years, as the number of predators increase, that this could have a negative effect. Even so, predation was the main cause of nest failure in all years and predator control, in the form of traps or snares, did not take place along set-aside strips where weasels, foxes and avian predators were frequently seen.

2.5.4.2 Yellowhammers

Results from this study highlighted that yellowhammer nest survival during the egg stage was likely to be affected independently by environmental factors such as temperature and rainfall. Stoate & Szczur (2001a) also recorded positive effects of temperature on yellowhammer nests. In the current study, the best MAM included rainfall only. Higher nest failure rates during colder weather and rainfall could be due to competition between incubation and foraging requirements. Eggs are likely to chill faster when the female is off the nest foraging and the availability of invertebrates is likely to be lowered due to their reduced activity.

Since the yellowhammer data set comprises a single breeding season the effects of predator control on nest survival rates could not be investigated although predation was identified as the main cause of nest failure. However, Stoate & Szczur (2001b) found, at Loddington, that yellowhammer nest survival was negatively correlated with carrion crow breeding density, and a negative relationship existed between overall nest survival rate and magpie (*Pica pica*) density for both the yellowhammer and song thrush (only significant for song thrush). Corvid density was not recorded as part of the current study although it is plausible corvids could affect nest survival rates of yellowhammers at Loddington.

Stoate et al. (1998) recorded no significant increase in yellowhammer survival rates with the introduction of predator control in 1993 at Loddington, although they note that their survival rates are higher than national data published at the same time. In the current study, habitat proportions surrounding the nest played no part in nest survival of this species. It is possible, however, that habitat factors were not investigated in the right way and could affect their survival. No other variables tested were found to influence yellowhammer nest survival. As this study only included a small data set collected over one season results should be treated with caution when comparing them to longer-term studies.

The current study's overall nest survival rate of 28.9% was lower than that reported by other studies, Stoate et al. (1998) 34–66% and Bradbury et al. (2000) 46%. This may be due to annual variation as found by Stoate et al. (1998) in 1995, due to cold weather. If the nest survival rate of this species at Loddington is a reflection of the local population to date, then at the current level of breeding success, the population is not self-sustaining.

2.5.4.3 Song thrushes

Several different variables independently affected song thrush nest survival during the various nesting stages (Table 11). However the overall MAM only included the position of the nest on the farm and the date incubation started. Predator control was an important factor affecting survival in the incubation stage and across all stages. Neighbouring farms did not exercise predator control and nests built on the border of the farm were more likely to be predated than those in the centre. A disused railway track and a wooded embankment, providing ideal nesting sites for many bird species, flank approximately one third of the border of Loddington. Hedgerows enclose the majority of the rest of the farm border. Woodland and the railway embankment also provide suitable habitat for both avian and mammalian predators. Stoate & Thomson (2000) found that song thrush at Loddington increased in abundance over time with game management, including predator control, and that the presence of carrion crows and magpies could reduce their nest survival rates (Stoate & Szczur, 2001b). Likewise Paradis et al. (2000) report a negative impact of corvids on song thrush reproductive output in their large-scale study of blackbird and song thrush.

In contrast, Gooch et al. (1991) analysed CBS and NRCS data for 15 songbird species (including skylark, yellowhammer and song thrush) and reported that although magpie numbers increased in Britain at an average rate of 4.5% per year they did not cause nest success declines between 1966 and 1986. Song thrush (and yellowhammer) nest success actually increased. The authors concluded there was no evidence to suggest that magpies had any deleterious effects on songbird populations or breeding success, although they recognised there may have been effects not detected in their study. The differences between the findings by Stoate & Szczur (2001b) and Gooch et al. (1991) may be due to the scale of the studies, one being on a local scale and the other on a national scale. Despite reported increases in corvid density on farmland between 1964 and 1993, avian predation cannot be solely responsible for the decline of many passerine species (Gregory & Marchant, 1996) and other factors, such as habitat effects, which may be inter-linked, are likely to be involved (Newton, 1998).

Habitats surrounding nests affected survival only in the egg stage, where the proportion of permanent pasture increased survival and cereal decreased it. This could possibly be related to earthworm availability close to

the nest. Pasture is known to be rich in earthworms (Tucker, 1992), the main food source of thrushes (e.g. Gruar et al., 2003), whilst cereals tend to be poorer. An incubating female may therefore spend less time foraging during incubation if there is more pasture surrounding her nest, thereby reducing the time the nest is exposed to predators and chilling. Once the clutch has hatched the male provides most of the nestling food whilst the female remains at the nest brooding till they are at least a week old.

The habitat type in which the nest was built affected nest survival in the nestling stage, which was found to be lowest in gardens ($0.923 \pm 0.234 - 8.4\%$) and highest in hedgerows ($0.959 \pm 0.006 - 27.7\%$). Gardens are more likely to be home to domestic cats (*Felis felis*), known to be a major predator of many passerine species (Churcher, 1987) and there is also likely to be a higher degree of inadvertent disturbance through human activity. However, as not all gardens were searched for nests, this low survival rate may not be representative of this particular habitat. Hedgerows at Loddington are mainly established blackthorn or hawthorn. Their thorns may offer some protection from certain predators. Rats and mice were occasionally seen working their way through hedgerows at Loddington and they could reach nests positioned on the inside of the hedge rather than on the outer edge.

The month in which nestlings were in the nest also affected their survival and nests at either end of the breeding season had lower survival rates than those in the middle. This could be a reflection of the reduced amount of nest concealment at the beginning of the season (although results show that concealment did not affect nest survival) or alternative sources of food for predators in the middle. It could be due to invertebrate abundance being lower at the beginning and end of the season, or due to parental quality. Adult song thrushes, being a multi-brooded species (Simms, 1978) are likely to be on their 3rd - 5th breeding attempt at the end of the season and may be physically out of condition. The significant interactions between months that young were in the nest and the nest site habitat could reflect a change in nest site habitat structure as the season progresses. It is possible that as vegetation grew and nest camouflage increased, from March onwards, nests may have been better protected both from nest predators and adverse weather conditions, improving nest survival rates.

Overall, once a nest contained nestlings, the outcome was not significantly influenced by the surrounding habitat composition indicating that nest failure was attributable to other factors, e.g. local weather conditions or predator control.

2.5.5 General issues

Despite minimising the negative effects of regular visits to nests, their potential for affecting nest survival should not be ignored. In particular, any damage to vegetation in the vicinity of nests could increase risks of detection by predators while frequent visits could affect adult behaviour. Nests in this study were checked more regularly than in many studies, possibly providing more accurate results on nest survival rates than those in studies that checked nests between every 3 - 7 days (e.g. Stoate & Szczur, 2001a), which could lead to an over-estimate in survival of each nest stage. It did not seem likely that the degree to which nests were checked negatively influenced survival, particularly because great care was taken not to attract attention to the nest or unduly disturb the adults. There was no indication at the time of checking that it was detrimental and very few birds abandoned their nests. Indeed, a UK study by Mayer-Gross et al. (1997) which examined the effect of nest visiting on some open nesting passerines (not including the skylark), concluded there was no overall effect of nest checking by experienced recorders on nest success. Other studies (e.g. Major, 1989) have reported that daily visitation significantly increases predation rates. Nichols (1984) also reported that daily or weekly visits to mourning dove (*Zenaida macroura*) nests resulted in similar nest success rates. Galbraith (1987) found that marking and visiting lapwing nests did not affect clutch survival, although his markings were around 20 - 30m from the nest site, not a few metres.

For each species, nests in the same fields, hedgerows, woods or gardens etc, are likely to be influenced by the same factors and therefore may not be independent from one another. For example, a predator working a hedgerow within its territory is likely to find most nests active at that time and as a consequence they are likely to be predated at the same time. In addition, nests found could be from the same pairs over the course of a season. The problem of nest level pseudo-replication is that it may artificially inflate the number of degrees of freedom and increase the likelihood of Type 1 errors (i.e. incorrectly rejecting the null hypothesis). This has to be taken into consideration when interpreting results.

2.5.6 Conclusions

Nest site location, and nest site characteristics, can affect subsequent nest outcome and nest survival rates. The decision where to place a nest could possibly be influenced by a number of factors such as habitat availability, breeding density, vegetation structure and invertebrate abundance etc, which in turn may affect nest survival rates, but this is different for each species.

For skylarks, nest sites contained more perennial grasses than control sites. Whether the perennial grasses offered structural support, protection from the weather or camouflage against predation was not determined. The non-significant trend for denser vegetation at the nest site, compared to the control sites, also possibly helps protect the nest and its contents from predation. Anecdotal evidence suggested that skylarks utilised winter cereal crops where patches of stunted growth occurred (pers. obs). Although nest densities were low in winter cereals compared to set-aside, they still provided nest sites both at the beginning and the end of the season, possibly due to the amount of exposed bare ground and the supporting structures available. No spring cereals were grown at Loddington because of the unsuitable clay soil. Kale and cereal set-aside strips, under Wild Bird Cover options, may become unsuitable for nesting towards the end of the season, particularly if they are very dense at the ground level. Grass set-aside with a shorter sward structure may then be utilised. The provision of set-aside in strips through field centres ensures that many birds have access to more than one habitat type for both nesting and foraging. However, vegetation structure has to be managed to allow a heterogeneous sward type to develop.

In addition to looking specifically at the skylark nest site vegetation structure, this study could also have examined the overall vegetation height within each habitat type (as Wilson et al., 1997a) and investigated its suitability for nesting. A study such as this may better assess which factors, regarding the microhabitat on offer to skylarks, are important in choosing a nesting site. Results could lend themselves to a better understanding of crop management for this species.

Hedgerow and boundary management is likely to have benefited both yellowhammer and song thrush by providing nest sites, but not necessarily in increasing their nest survival rates. Woodland management is also

likely to have helped the breeding song thrush population by providing nest sites that offer a degree of shelter and protection as the season progressed. Habitat compositions around nests at Loddington influenced song thrush nest survival more than that of skylark and yellowhammer. Increases in the area of permanent pasture around the nest positively influenced their nest survival, whereas increases in cereal crops surrounding nests decreased nest survival rates during the incubation stage. Managing these habitat types in a sympathetic manner for song thrushes may therefore increase survival rates.

Of the three study species, skylarks were least prone to nest failure whereas for the other two species over 70% of nests failed. For all three species, predation was the main cause of nest failure despite their different nesting ecology's. Therefore it would appear that habitat management and predator control at Loddington are the most likely factors to improve nest survival. In order for nests lost to predation to be recouped, birds must have access to other suitable nesting places throughout the entire nesting season.

Appendix 2**a. Skylarks**

Outcome	2000	2001	2002	Total	Total %
Success	9	17	6	32	45.71
Egg predation	5	2	2	9	12.86
Chick predation	6	6	4	16	22.86
Abandoned	1	2 (1 egg and 1 chick)	0	3	4.35
Broods starved	1	2	1	4	5.71
Weather	3 (1 egg, 2 chicks)	0	1	4	5.71
Agricultural losses	0	1 (egg stage)	0	1	1.42
Unknown	1	0	0	1	1.42
Total	26	30	14	70	100

b. Yellowhammers

2000	Success	Egg predation	Chick predation	Unknown predation	Abandoned	Broods starved/died	Unknown	Weather	Total
Outcome	10	4	8	2	1 (egg)	7	2	1 (chick)	35
Total%	28.57	11.43	22.86	5.71	2.86	20	5.71	2.86	100

c. Song thrushes

Outcome	2000	2001	2002	Total	Total %
Success	23	37	27	87	29.29
Egg predation	10	35	30	75	25.25
Chick predation	13	27	18	58	19.52
Unknown predation	0	3	7	10	3.37
Abandoned	0	18 (17 egg stage, 1 chick stage)	21 (18 egg stage, 3 chick stage)	39	13.13
Broods starved/died	0	0	2	2	0.67
Unknown	1 (chick)	2	15	18	6.06
Weather	4 (egg stage)	4	0	8	2.69
Total	51	126	120	297	100

Appendix 2, Tables a, b and c: Outcome of skylark, song thrush and yellowhammer nests by year. Nests were considered successful if one or more chicks fledged. Egg predation refers to nests predated in the nest stage, Chick predation refers to nests predated with nestlings, and unknown predation refers to nests lost to a predator but in what stage is unknown. 'Weather' refers to nest failures caused by bad weather such as heavy rain, snow etc.

Appendix 2, Plate 1. Demonstrating the use of the cover density board to measure vegetation density at foraging or nest sites.



CHAPTER 3

HABITAT USE BY NESTING AND PROVISIONING BIRDS

3.1 Summary

1. Habitat use was studied for breeding skylark and song thrush over a three-year period and yellowhammer for a single season in 2000. Radio-telemetry was used to study the song thrush, due to its secretive nature, but direct observation was used for skylark and yellowhammer since they were highly detectable on the farm landscape.
2. This chapter aims to assess habitat use by nesting females (whether birds surround their nests with certain habitat types on the farm landscape more than would be expected relative to availability) and habitat use by provisioning adults (whether they foraged in certain habitats around the nest more than would be expected relative to availability). The hypothesis that provisioning birds would use wildlife crops and semi-natural habitats more than commercial crops, relative to their availability, was tested.
3. A comparison was made between foraging habitat use of provisioning skylarks and yellowhammers during 2000. Although there have been many foraging studies carried out on both species on different types of farmland, this is the first that aimed to simultaneously assess habitat use of farmland incorporating habitat features developed as potential agri-environment scheme options by both species on the same farm.
4. Habitat composition around nests of each species was not random. Generally, the habitat around each nest differed significantly from random with respect to availability. Set-aside and cereals were more common around skylark and yellowhammer nests and woodland and boundary habitats more common around song thrush nests.
5. Skylarks, yellowhammers and song thrushes did not forage randomly across the farm landscape available to them. Skylarks and yellowhammers made particular use of different types of set-aside when feeding nestlings. Yellowhammers used cereals, beetle banks and cereal based set-aside more than would be expected relative to availability. Skylarks primarily used managed set-aside, but also used beetle banks, grass set-aside and cereals more than expected. Song thrushes preferred woodland and boundary habitats when provisioning both nestlings and dependent young.
6. The simultaneous assessment of skylark and yellowhammer habitat use showed each species utilised habitats differently for foraging. Skylarks used kale set-aside more than expected and yellowhammers used cereals more than expected relative to their availability.

7. These results suggest that, at Loddington, for skylarks and yellowhammers wildlife crops sown on set-aside and other managed set-aside types are important when they have chicks in the nest. Song thrushes did not use wildlife crops or indeed any set-aside type more than would be expected relative to their availability, but woodland and managed hedgerows and field margins were important. Each species benefited from habitats that maintained heterogeneity, received low chemical inputs and potentially held a high abundance of invertebrate chick foods. The implications of this will be discussed in further chapters.

3.2 Introduction

Assessment of habitat use by farmland birds is of particular importance when trying to understand and reverse their declines, mainly because bird population declines have been sharpest on farmland than any other habitat type in Great Britain (Fuller et al., 1995, also see Chapter 1). The skylark, yellowhammer and song thrush are frequently cited as common farmland bird species. Populations of species such as these that specialise on farmland in Britain have declined more, on the whole, than habitat generalists (Siriwardena et al., 2001).

Studies on habitat association or use have taken place at both national and local scales (i.e. large and small). National scale studies often determine habitat use using territory density data or survey plots collected through BTO surveys (e.g. Chamberlain & Gregory, 1999; Chamberlain et al., 1999a; Browne et al., 2000; Siriwardena et al., 2000b). Farmland skylarks are associated primarily with set-aside, cereal fields and spring-sown crops during the summer, and winter cereal stubbles and set-aside during the winter (Chamberlain et al., 1999a; Vickery & Buckingham, 2001; Donald et al., 2001a; Donald et al., 2001b). Yellowhammers are associated with hedgerows and grass margins in the summer (Morgan & O'Connor, 1980; Mason & Macdonald, 2000; Perkins et al., 2002) and winter, whilst the song thrush is closely tied to tall hedgerows, woodlands, gardens and pasture (Sparks et al., 1996; Mason, 1998). Small-scale intensive studies can further determine which habitats are of particular importance to different species within that locality, and help formulate management plans for different species, to help re-address population losses within defined areas (see Sparks et al., 1996; Evans et al., 1997; Mason, 1998; Aebischer et al., 2000; Brickle et al., 2000). Skylarks prefer to forage in set-

aside, grass margins and tracks (Wilson, 2001), yellowhammers utilise broadleaved crops, then barley and then wheat across the breeding season (Stoate & Szczur, 1997) and song thrushes forage in woodland, wet ditches and gardens (Peach et al., 2002; Peach et al., 2004). Local scale studies across a wide-range of regions on the same study species can help establish whether the species requirements remain the same or vary spatially and are factors important when formulating species management plans.

The skylark and yellowhammer are cereal specialists (Kyrkos et al., 1998; Stoate et al., 1998; Bradbury & Stoate, 2000; Donald & Vickery, 2000; MacCleod, 2001; Wilson, 2001; Morris et al., 2001a; Morris et al., 2001b). More skylarks are found in cereals than in any other farmland habitats, although territory densities are frequently low relative to other habitat types and often decrease over cereals in the course of a season (Donald & Vickery, 2000) but not always (Mason & Macdonald, 2000). Yellowhammers are associated with boundary habitats (such as hedgerows, grass margins), densities increasing with hedgerow length and area of cereal present (Andrew, 1956; Kent, 1964; Biber, 1993a; Kyrkos et al., 1998; Bradbury et al., 2000). The association of these two farmland specialists may in part be due to the fact that cereals cover such a large area of farmland and on lowland farms represent the largest single component (Donald & Vickery, 2000). Habitat use of set-aside during the breeding season and over winter is also known to benefit both these and other species (Watson, 1992; Draycott et al., 1997; Poulsen et al., 1998; Buckingham et al., 1999; Browne et al., 2000; Donald & Vickery, 2000; Henderson & Evans, 2000; Henderson et al., 2000a; Henderson et al., 2000b; Vickery & Buckingham, 2001; Donald et al., 2001b; Firbank et al., 2003; Hancock & Wilson, 2003). Lowland grasslands are generally avoided in summer (Mason & Macdonald, 2000; MacCleod, 2001; Morris et al., 2001a) and over winter (Wilson et al., 1996), but both skylarks (Browne et al., 2000) and yellowhammers use ungrazed grass fields more than grazed fields (Wilson et al., 1996).

The declines of song thrush populations are also higher on farmland than other habitats (Fuller et al., 1995), but this species occurs in higher proportions in woodland and human habitats compared to farmland (Gregory & Baillie, 1998; Mason, 1998, 2000). Song thrushes may be less susceptible than skylarks and yellowhammers to further declines nationally since gardens and parks act as a last refuge (Mason, 1998) and there is limited evidence to suggest that changes in agriculture have contributed to their decline (Thomson & Cotton, 2000). Breeding farmland song thrushes forage mainly in woodland, grassland, wet ditches and

gardens (Peach et al., 2002; Peach et al., 2004). A study of invertebrate-feeding birds, over-wintering on farmland in southern England, found that permanent pasture held the highest densities (including song thrush) (Tucker, 1992), which was also supported by Wilson et al. (1996). Sparks et al. (1996) found that song thrushes were closely associated with woodland, permanent pasture was indicative of their presence, and tall hedges bordering permanent pasture were preferred, probably because they were associated with woodland. Other winter studies found brassicas were the preferred habitat type (Wilson et al., 1996; Buckingham et al., 1999; Henderson & Evans, 2000). Compared to skylarks and yellowhammers, set-aside was used relatively little by song thrushes (Henderson & Evans, 2000) and winter cereals were generally avoided in both the winter and summer (Wilson et al., 1996; Buckingham et al., 1999; Peach et al., 2002; Peach et al., 2004).

It is therefore important to assess habitat use at both the local and national scale and to determine firstly, which habitats are used more by particular species than others, and secondly, why this is so (Chapter 4). Thus, just as nest site selection is a fundamental part of our understanding of habitat choice by any bird species for sympathetic land management (Chapter 2), so too is the precise pattern and nature of habitat use during the critical period of provisioning young (this chapter). The female (skylark, yellowhammer and song thrush) builds the nest, so ultimately decides where the nest will be positioned within the territory defended by the male, but both parent birds feed their young. Since relatively few intensive studies on foraging habitat selection have been carried out at a single site on the three species on lowland farmland (Stoate & Szczur, 1997; Perkins et al., 2002) the opportunity to simultaneously assess the use of farmland by skylark and yellowhammer at Loddington, using data collected over a single season was taken. Loddington implemented simultaneously many habitat management changes (see Boatman et al., 2000), which are thought to have benefited numerous bird species, so the hypothesis, 'Birds use wildlife crops and semi-natural habitats more than commercial crops, relative to their availability whilst provisioning young in the nest,' was tested.

Following on from Chapter 2, which investigated nest site location, this chapter aims to i) examine habitat use around nests by breeding skylark, yellowhammer and song thrush, ii) examine habitat use by provisioning birds around the nest and at the study site level, to see whether habitat use is non-random and iii) simultaneously assess habitat use by breeding skylark and yellowhammer. Analysis takes into account all nests built and those nests that survived the laying and incubation stage separately.

3.3 Methodology

3.3.1 Collection of data

The location of the study site is described in Chapter 1, section 1.6. All nests were located and monitored using the methods described in Chapter 2, section 2.3.1. Nests involved in foraging watches were used to examine foraging habitat use by adults whilst provisioning young. The methodology for skylark and yellowhammer foraging watches is described separately to that for song thrush.

3.3.1.1 Skylark and yellowhammer foraging watch methodology

All skylark and yellowhammer nests with nestlings between 2 - 7 and 3 - 10 days old respectively were used in foraging watches. These ages were considered acceptable, as they were not likely to induce abandonment or premature fledging. However, during 2001 and 2002, radio tags were fitted on seven-day old skylark nestlings so watches took place on nests with nestlings between the ages of 2 and 6 days old for these years. Skylarks and yellowhammers are fairly conspicuous in the farm landscape and could be observed foraging in a variety of habitats.

Three 90 - minute observation periods of foraging habitat use by adult birds were conducted during dry weather conditions, starting at 0600, 1000 and 1400hrs. A small microphone placed next to the nest enabled all visits by provisioning adults to be recorded by the observer sitting in a vehicle up to 75m away (Stoate et al., 1998). A watch commenced when a parent bird arrived at the nest with food. During a watch, every location to which a provisioning adult flew to forage was recorded on a map. For each location, the distance from the nest, habitat type and time were noted. The number of provisioning visits to the nest was also recorded. This may have been different to the number of foraging places recorded if a bird was not seen landing.

Most birds foraged in a single habitat type and, for the purpose of this study, were considered to forage in the first place they landed. Foraging distance was defined as the maximum straight-line distance from that point

to the nest. Distance was either measured directly on the ground with a trundle wheel or by plotting the nest and foraging point on a Geographical Information Systems (GIS) map, in MapInfo version 7 (MapInfo, 2002), and measuring the distance directly from the map. If a bird could not be seen landing to forage, the place was recorded as 'unknown location' and was not included in the analysis.

Yellowhammers were studied in 2000 only, mainly due to developments within the song thrush project resulting in more effort being allocated to the latter species.

3.3.2 Skylark and yellowhammer data analysis

3.3.2.1 Habitat use by breeding skylarks and yellowhammers

Habitat use by breeding skylark and yellowhammer was examined at Loddington by comparing the composition of habitats surrounding *each nest found* with the availability of habitats on the study site. For each nest, the proportional area of habitats within an established radius around the nest was calculated using the 95th percentile distance of all foraging trips across all years to define the area 'used' by breeding birds. The radius was calculated as 118m for skylarks (during the three year study period) and 146m for 2000 only, to allow a comparison with yellowhammer habitat use in 2000 (see Table 4 for foraging distances between years).

For yellowhammers the 95th percentile distance was 191m from the nest in 2000. The area of habitat available to breeding birds included the whole of the study area and some of the neighbouring fields. MapInfo calculated the areas of each habitat within the circle and on the study site and compositional analysis was used to investigate differences in use by nesting birds (see Chapter 1, Appendix 1). The foraging range for skylarks and yellowhammers in 2000 was 6.38ha and 11.37ha respectively and for skylarks from 2000 – 02 was 4.37ha. A year effect was tested for on skylark data, to see whether habitat use differed between years.

3.3.2.2 *Habitat use by foraging skylarks and yellowhammers*

Skylark and yellowhammer habitat use by provisioning birds was examined at Loddington by comparing the habitats in which birds were directly observed to forage with the availability of habitats around the nest site using compositional analysis (see Chapter 1, Appendix 1 and Figure a). For each nest, the proportion of foraging visits to each habitat was calculated and compared with the proportional availability of habitats within an established radius around each nest. The radius was determined by calculating the 95th percentile distance of all foraging trips across all years, as above, and areas under the circle were calculated in MapInfo. A year effect was tested on data collected across the three years for skylark, to see whether habitat use differed between years.

3.3.2.3 *Comparison of habitat use by foraging skylarks and yellowhammers*

Compositional analysis was used to test whether habitat use differed between skylark and yellowhammer, using species as a factor to determine where the differences, if any, lay (see Chapter 1, Appendix 1). Where habitat use was significantly non-random, paired t-tests were performed on each log-ratio to compare relative use of each habitat with all other habitats individually in order to rank habitats according to difference in relative use between species and within species. Nine habitat categories were included in the analyses (Table 1).

3.3.3 Song thrush

A different approach to that adopted for skylark and yellowhammer was used to investigate song thrush foraging habitat use whilst provisioning chicks. This was primarily because these birds are known to forage in edge habitats and are generally not observed when foraging (except in gardens or other open areas), unless disturbed. The males are known to provide most of the food items (Hartley, 1967), whilst the female will often brood chicks tightly up to 9 - 10 days old (pers.obs).

Table 1: Habitat categories included in skylark and yellowhammer habitat use analysis.

Habitat category	Abbreviation	Habitats included
Beetle banks	BB	Sown with a variety of grasses on set-aside (see Boatman <i>et al</i> 2000).
Broadleaved crops	BLCrop	Oilseed rape, winter and spring beans
Cereal	Cereal	Winter wheat, winter barley, winter oats
Cereal set-aside	CSA	All years (1 st , 2 nd , 3 rd)
Grass set-aside	GRSA	Including grass tracks
Kale set-aside	KSA	All years (1 st , 2 nd , 3 rd)
Other crop set-aside	Othcropsa	Planted with crop including wild bird plots, sorghum, artichoke and partridge mixes, wildflower mixes, mustard
Other	Other	Permanent pasture, woodland, hedge, ditch, ponds and streams, buildings, concrete roads etc
Other vegetation	Oth_veg	Grass strips, non set-aside beetle banks, tall and short rough grass embankments, field margins, verge, herbaceous vegetation and short grass

In order to investigate song thrush foraging, it was necessary to use radio-telemetry to follow foraging birds. In the first year of the study a pilot project was undertaken to assess the feasibility and practicality of this monitoring technique. A licence from the BTO was obtained to attach up to 5 radio-tags to breeding song thrushes. Birds were caught in mist nets and 1.9g back-pack harness-mounted TW-4 radio-tags with a range of around 600m and a life of over 60 days were attached. In the final field season, tags were fitted with thermistors to indicate mortality. Radio-tags weighed less than 4% of body weight. They were made by Biotrack and the back-pack harness, designed with a weak link, was followed from Hill (1998). Training was provided by Hill to make back-pack harnesses and then were subsequently made by the author. Hill *et al.* (1999a) had shown that this harness design did not influence breeding performance in blackbirds (*Turdus merula*) and song thrushes, although it is not known whether foraging behaviour is affected. In the final two years of the project, licences to tag 20 birds were obtained for each year. In the first year, cold trapping of males singing within territories was adopted and resulted in only two birds being caught despite many trapping hours. The trapping strategy was therefore changed once the breeding season was underway and male song thrushes provisioning nestlings were targeted at the nest. Extreme care was taken not to damage vegetation around the nest sites. Trapping took place, in dry weather only, when chicks were between two and 10 days

old (day of hatch = 0 days old). Nets were left up for one hour at a time, once a day until the targeted bird was caught or the nest failed or chicks were too old to use for foraging watches.

Once a bird was caught in the net, it was removed and the nets were immediately furled. Birds were processed at least 30m from the nest. If the bird was not already ringed, a BTO metal identification ring with a year colour code was put on one leg and a unique two-ring colour code on the other leg. Weight, sex and wing length were also recorded. In the second and third year of the study females were often released after ringing with no radio-tag since males were preferred for data collection. Tagged individuals were placed on the ground for release in an open space within their territory and away from any roads. The movements of some birds were unbalanced immediately after tag attachment so all birds were regularly located using the receiver until their flight was unrestricted.

3.3.3.1 Song thrush foraging watch methodology

In order to examine foraging habitat use, a fix was taken every 20 minutes from each tagged bird for three, three-hour periods during the nestling stage (similar to the skylark and yellowhammer) to obtain spatially independent fixes. This started the day after the tag was put on and fix sessions began at 0600, 1000 and 1400 hrs. At least thirty fixes were obtained in order to provide the minimum fix requirement for subsequent foraging range analysis (Kenward, 2001), unless the bird disappeared or was predated. A fix was considered to be spatially independent after 20 minutes from the last since the bird had time to leave the nest, forage, return to the nest and leave again. Fixes were collected using the triangulation system with three-element hand-held Yagi antennae and receivers (White & Garrot, 1990; Kenward, 2001). It was recognised that errors may arise in the estimated location due to bearings not being taken simultaneously. It generally took between 3 - 6 minutes to complete a fix (93% of all fixes taken), depending on the signal and availability of suitable places from which to take bearings. Birds that had tags put on but had no nest or nests that failed during the nestling period had up to three fixes a day recorded until the battery died or the bird disappeared. One set of 10 post-fledging fixes was also recorded two weeks after successful fledging of that bird's brood. During the radio-telemetry session the aim was not to disturb the foraging bird, which would obviously bias the habitat in

which the bird foraged. Therefore a minimum distance of at least 50m from the bird was maintained. Sites where fixes were recorded were generally at least 30 - 40m apart and did not cross the flight path to the nest.

3.3.3.2 Triangulation

During the field season fixes were plotted by hand on to a map of the area surrounding the bird's nest, taken from MapInfo, over-laid with a 10m x 10m grid. Plotting the three bearings produced an error triangle. As a guide to where the bird was most likely to be foraging, the centre of the triangle was taken as an estimate of where the bird was at that time (White & Garrot, 1990), although a triangle could include more than one habitat type. The primary purpose of plotting the fixes by hand was to enable worm samples to be taken during the nesting period of each nest (i.e. the sample unit) (see Chapters 4 and 5). The centre of the triangle was found by measuring half way along two sides of the triangles and drawing a line to the opposite corner. The resulting intersection indicated the centre of the triangle. Grid references were read to the nearest 10m on an overlaid grid. If a fix did not triangulate but bearings one and two or two and three crossed, the point where the lines crossed was taken as the position of the foraging bird. A bird may have been disturbed or flown back to the nest, resulting in a non-triangulation. The number of grid intersections was also recorded as a measure of how large and accurate the fix triangle was.

Throughout the project an attempt was made to validate fix position. Tags were placed in different habitat types and fixes taken to locate them. The centre of the triangle was compared with the position of the tag when it was recorded with either a hand-held or differential Global Positioning System (GPS). Approximately 7 - 8 times out of 10 the tag was plotted in the correct place, but was generally never more than 15 metres away from its true location. In addition to this, at the end of the three-hour radio-telemetry session, the bird was often flushed out of the habitat it was in to determine the accuracy of the last fix.

3.3.3.3 Defining habitat use

Once the three years of foraging data had been collected, MapInfo was used to plot only bearings that were known to triangulate on a more refined map of the study area. Julie Ewald (Game Conservancy Trust) wrote

the relevant program. Although this method provided a more conservative estimate of foraging bird positions and habitat use, it was deemed to be more accurate. From the plotted triangles the centre of the triangle was found and the habitat type at this point was listed. The area of each triangle (hectares), the distance of all vertices to the nest (in a straight line), the distance of the centre of the triangle to the nest, the habitat types and their areas (hectares) under each triangle, the number of 10m x 10m grid intersections within each triangle and the exact grid reference of the centre of the triangle were also recorded.

“If habitat patches are large relative to telemetry error, misclassification will have little effect on estimated habitat use or selection unless animals occur at the edge of the habitat” (Samuel & Kenow, 1992). Therefore, if a fix triangle contains only one habitat type then it is almost certain the bird is within that habitat type, but if it is large and contains several habitats then habitat allocation may be biased. Larger triangles cover more area and may contain more than one habitat type, possibly making them less accurate than small triangles. Therefore by accepting the centre of the triangle as a measure of where the bird was actually foraging, interpretation was open to error, especially if there were smaller habitat areas contained within it. Statistically, it was logical to assume that a bird would be present in the largest habitat area within the triangle, since probability would suggest this to be most likely. MapInfo was therefore used to determine the largest habitat area within each triangle and the habitat type in the centre of the triangle. The two were compared and 92% of the time the centre of the triangle did fall under the largest habitat area, which was considered to be sufficiently accurate when taking soil cores for worm samples (see Chapter 4 and 5). However, it showed that the largest habitat area within a triangle was not always accurate in determining where the bird was said to be, possibly distorting the measure of habitat use (particularly as song thrushes forage in linear habitats such as ditches and hedges). Triangulation error means that the middle of the triangle is not an exact point but the actual location lies somewhere within the error area (Springer, 1979). In addition to this, if the centre point in the triangle borders another habitat, the bird could be in either habitat type, again distorting interpretation of habitat selection (Nams, 1989).

Consequently in order to *define foraging habitat use* by provisioning song thrushes in the current study, it was decided to use the triangles themselves as a measure of use. Since some triangles contained a large number of grid intersections, the intersections were used as a measure of error. The number of grid intersections ranged

from 0 - 76 and 90% of triangles (out of 1030 triangles made; 296 home range, 593 foraging range and 169 post fledging) had fewer than 19 intersections, and 50% had fewer than 3. Triangles with large areas were considered more poorly defined than those with small areas and fewer grid intersections, so a limit of 25 grid intersections was set to determine which triangles were to be used in the analysis (totalling 94% of fixes plotted). The proportions of different habitat types in each triangle, for each bird, were calculated and the proportions of each habitat were averaged across triangles per bird to obtain an overall measure of foraging habitat use. The average size of error triangle used in analysis was 0.035ha, ± 0.002 (Table 2). MapInfo plotted a total of 593 provisioning triangulations and 558 (94%), with fewer than 26 grid intersections, were used in the analysis. Figure 1 shows the percentage of grid intersections under fix triangles, either for provisioning, home range or post fledging, with fewer than 26 grid intersections.

Table 2: The mean area of error triangle, using those with fewer than 26 grid intersections, during the different stages of fix taking (± 1 SE). 0.03ha roughly equals a 17m x 17m square.

Triangle type	Mean area (hectares)	SE	Number of fixes	Range (hectares)
<i>All</i>	0.035	0.002	963	0 - 0.229
<i>Provisioning</i>	0.035	0.020	558	0 - 0.229
<i>Post-fledging</i>	0.028	0.003	162	0 - 0.221
<i>Home range</i>	0.041	0.003	241	0 - 0.228

Schmutz & White (1990) state there is an increase in error, reducing the accuracy of the data, with a time delay between bearings. Therefore using all fixes used in the analysis ($n = 963$) the mean size of error triangle (ha) was plotted against the time taken to take each fix (using three bearings) (Figure 2). The graph showed no obvious influence of time taken to fix a bird on the accuracy of the fixes, i.e. mean error triangle size (ha). 93% of them took between 3 - 6 minutes to take.

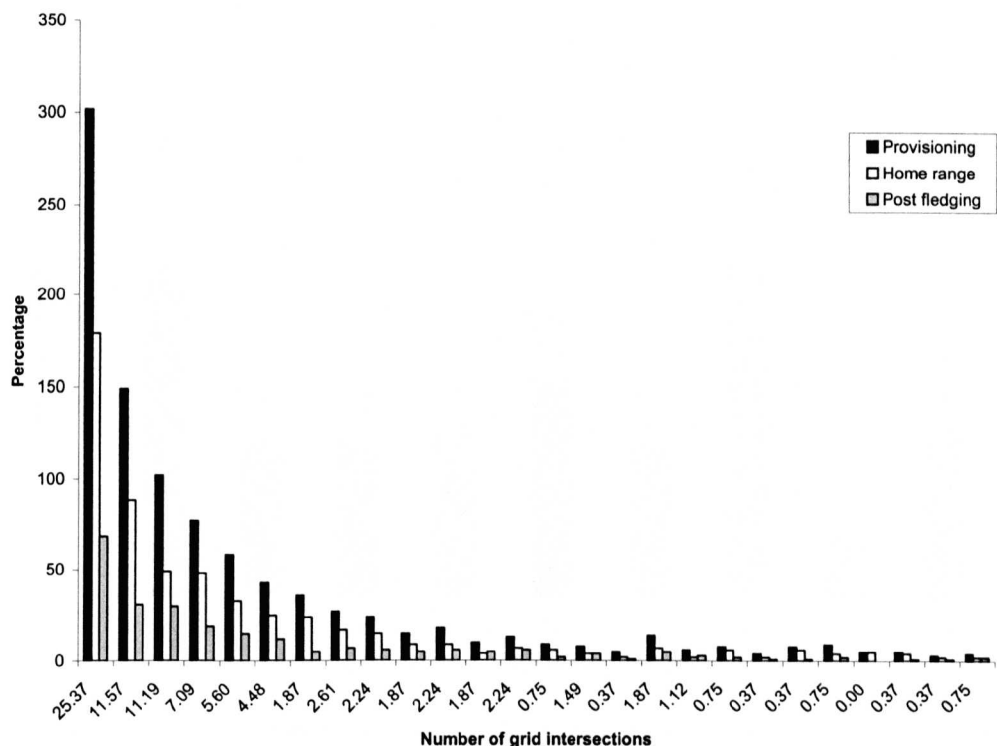


Figure 1: Fix accuracy, determined by the number of grid intersections within the error triangle. The mean area of error triangles for fixes with fewer than 3 intersections was 0.007ha (n = 317) for provisioning triangles, 0.007ha (n = 130) for home range triangles and 0.007ha (n = 107) for post-fledging triangles.

In order to define foraging *habitat availability* for each song thrush nest, two methods were adopted.

Method 1. To *define foraging habitat availability for provisioning birds* a minimum convex polygon (MCP) was created using the outer vertices of the foraging triangles for each bird (rather than the radiolocations themselves) (Aebischer et al. 1993a). This method was used for analysis in section 3.4.2.4 and 3.4.2.5 (habitat use by foraging birds and for post-fledging comparisons).

Method 2. The 95th percentile area of the provisioning MCPs was determined and a common radius calculated from the equation Πr^2 . This distance was then used as a common radius around *every nest to define habitat availability around that nest* for analysis in section 3.4.1.3 (habitat use by breeding birds). This was calculated as 118m.

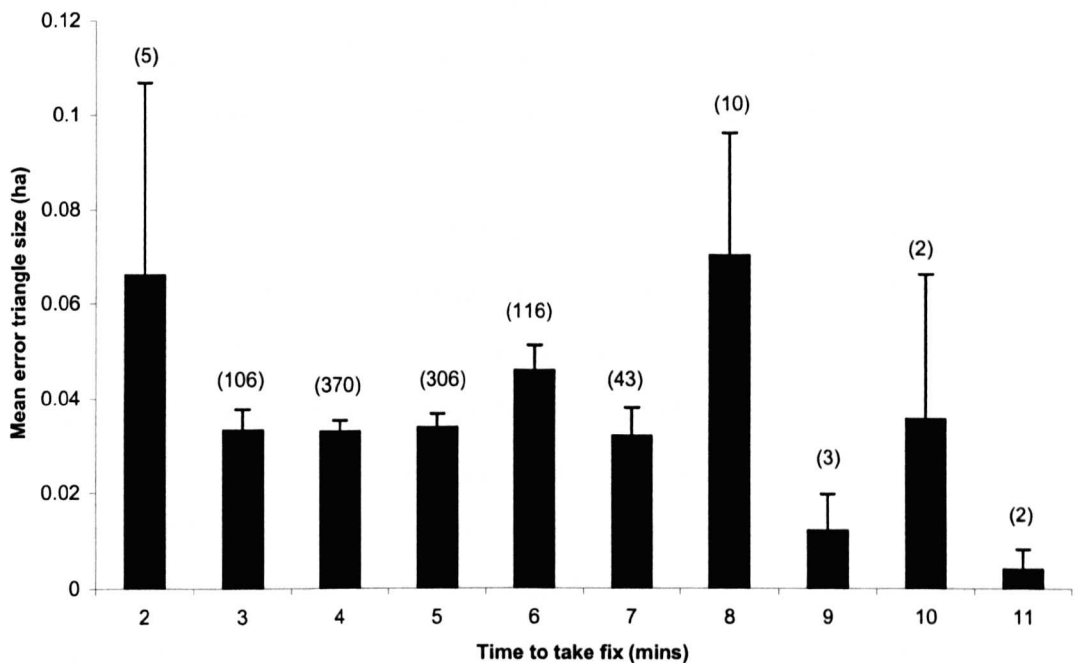


Figure 2: Mean size of error triangle (ha) against time taken to take the fix (minutes), \pm 1SE, using error triangles with fewer than 26 grid intersections. Figures in parenthesis are sample sizes.

In contrast to the skylark and yellowhammer it was unrealistic to use the 95th percentile distance to calculate a common radius around the nest, particularly as the centre of the triangle was not used to determine the bird’s position. By using the maximum distance from the nest to the furthest triangle vertex (one value per nest) and calculating the 95th percentile distance of those values across nests calculated a foraging radius of 298.68m, providing an area of 28.07 hectares of habitat available around each nest. Hence, females would rarely visit much of that area. Song thrushes travel approximately 100m from the nest during the nesting period (Peach *et al.*, 2004) so the 118m-radius set around each nest is likely to be a more accurate representation of habitat availability to breeding birds than a radius of 298.68m.

A year effect was tested for on song thrush data (n = 22) collected in 2000, 2001 and 2002.

MCPs describe the outer limits of an animal’s movements and are the smallest polygons with all external angles greater than 180 degrees that can be fitted around a set of fixes (Mohr, 1947). They are the most widely used home range estimator but the area and shape of the polygon is heavily influenced by outlying fixes and do not show how intensively the animal uses certain habitats within it (Harris *et al.*, 1990). MCPs were used

for this analysis since analysis followed the procedure laid down by Aebischer et al. (1993) for using compositional analysis. When the size of the MCP is plotted against the number of fixes, the area is unlikely to increase after a certain number of fixes have been collected (i.e. sampling saturation (Kenward, 2001)). For each song thrush, at least 30 foraging fixes were collected based on the knowledge that this was enough to reach sampling saturation for many species (Kenward, 2001), including song thrush (Hill, 1998). However, provisioning fixes were collected over a three-day period, rather than collecting up to 3 fixes a day as Kenward (2001) suggests, to enable 30 fixes to be collected over the nestling period. When the foraging data were plotted using MapInfo only bearings that triangulated were used in the analysis reducing, and varying, the number of fixes per bird to below 30 in some cases. Below 30 fixes, home range estimation can be reduced with the number of fixes made, although habitat analysis is sometimes still carried out (Carroll et al., 1995; Anders et al., 1997). MCPs are generally robust when fix numbers are low (Harris et al., 1990). The mean number of fixes per bird, for the current study, was 26 when using MapInfo. Another issue, accounting for the expected difference in size of the foraging MCP, relates to where the bird was considered to be foraging. In the foraging range plotted by hand during the field season, the bird was taken to be in the centre of the triangle for invertebrate sampling purposes. However, when plotting them in MapInfo the furthest vertices of the foraging triangles were used. This increased the average foraging MCP from 0.81ha to 1.87ha ($n = 22$).

Rather than refer to the area of this MCP as the 'home range', 'an area repeatedly traversed by an animal' (Kenward, 2001), it will be referred to as a 'foraging range' or 'foraging MCP', an area where birds foraged for food for nestlings around the nest site. This is more in line with the 'home range' definition of Burt (1943) as 'the area traversed by the individual in its normal activities of food gathering, mating and caring for young'. Data, collected once chicks had fledged, may show that the 'foraging range' expands and birds use different parts of their 'home range' according to the stage of the breeding cycle. 'Home range' areas will refer to the MCP surrounding fixes taken from birds during periods of no nesting activity.

The proportional habitat types under song thrush foraging MCPs were calculated and adopted to compare habitat use versus habitat availability at two levels: (i) between foraging triangles (using the proportions as explained above to define used area) and foraging MCPs (the available foraging area) and (ii) between

foraging MCPs (used area) and the study area (available area). Ten habitat categories were included in the analysis (see Table 3).

Table 3: Habitat categories used in the analysis of song thrush habitat use.

Habitat category	Abbreviation	Habitats included
All set-aside types	Allsa	All set-aside types found on the study site
Broadleaved crops	BLCrop	Oilseed rape, winter and spring beans
Boundary	Bound	Field margin, verge, hedge and ditch
Cereal	Cereal	Winter wheat, winter barley, winter oats
Garden	Garden	Mown grass, gardens and graveyard
Grass vegetation	Grass veg	Field entrances, grass strips, short grass, tall rough grass and non set-aside beetle banks.
Herbaceous vegetation	Herb veg	Embankment, tall and short herbaceous vegetation, short rough vegetation
Other	Other	Buildings, concrete, roads, stone walls, tennis courts, swimming pools, driveways, pavements, ponds and streams
Permanent pasture	PP	All grazed fields
Woodland	Wood	Old and new woodland

3.3.4 Song thrush habitat use data analysis

3.3.4.1 *Habitat use by breeding song thrushes*

In order to examine habitat use by breeding female song thrushes, the composition of habitats around *all nests* found was compared with the general availability of habitats across the study site (see 3.3.3, Method 2). The radius of the 118m circles would not encompass all foraging triangles, but defined an area around the general vicinity of the nest within the foraging range (incorporating 4.41ha). Compositional analysis was used to compare proportional habitat use (the area around each nest) with proportional habitat availability (the area of the study site). Data collected across the three-year study period were used in the analysis (see Table 4)

3.3.4.2 *Habitat use by provisioning song thrushes*

In order to examine habitat use by provisioning song thrushes, the composition of habitats within the foraging triangles (i.e. proportional use) was compared with the composition of habitats within the foraging MCP (i.e. proportional availability) using compositional analysis. Compositional analysis was also used to investigate habitat use by provisioning song thrushes by comparing the foraging MCP (i.e. used habitat) with the general availability of habitats across the study site (i.e. available habitat). Data collected across the three-year study period were used in the analysis (see Table 4 and Chapter 1, Appendix 1- Figure c).

3.3.4.3 *Habitat use by song thrushes post fledging*

To examine changes in foraging ranges once chicks left the nest, a series of 10 post-fledging fixes were taken 1 - 2 weeks after the fledge date, on one day only (due to time constraints). Fixes were taken using the same methodology as in section 3.3.3.1. Post-fledging fixes were only taken for nests that successfully fledged young ($n = 15$). Post fledging fixes plotted by MapInfo allowed the new MCP boundary to be drawn around the outside vertices of both the provisioning and post-fledging triangles. The difference in MCP size was compared using a paired t-test. To examine whether habitat use changed during this period compositional analysis was used (see Table 4). Habitat compositions used and available were calculated as described earlier.

3.3.4.4 *Home range areas of non-provisioning birds*

A small number of home range fixes were collected from birds that either did not attempt to nest or were between nest attempts, in 2000 ($n=2$) and 2001 ($n=7$). Two sets of data were collected from female birds. Full sets of 30 fixes were not collected for all birds because they either started to nest, disappeared or died, hence limiting sample size and any analysis. Nine sets of data were used to compare range sizes. The resulting home range areas calculated are a representation of song thrush home ranges at Loddington, which are unlikely to be comparable to studies using 30 fixes.

Table 4: Distinguishing between the three types of composition analysis carried out on the song thrush habitat use data. Further descriptions of the analysis are found in the text of section 3.3.4. MCP = minimum convex polygon.

Analysis involving data from ...	Nests involved in analysis	Analysis level	Habitat use analysis	Why?
Breeding song thrushes (section 3.3.4.1)	All nests found regardless if nest active or not when found. No telemetry required. No tagged birds required.	Nest level	To compare the composition of habitats around all nests within 118m radius of nest with the composition of the study area.	To investigate whether song thrushes position their nests randomly across the habitats available to them.
Foraging/Provisioning watches (section 3.3.4.2)	Nests involved in foraging watches only (i.e. when tagged birds provisioning nestlings monitored).	Nest level	To compare the composition of habitats within the foraging triangles with the foraging MCP range.	To investigate whether birds provisioning nestlings randomly utilise each foraging habitat within the foraging MCP
		Study site level	To compare the composition of foraging MCP range with the composition of the total study area.	and whether the foraging MCP is randomly established across the study site.
Post-fledging – provisioning fledglings (section 3.3.4.3)	Nests involved in post-fledging watches and foraging watches (i.e. when tagged birds feeding young).	Study site level	To compare the composition of post-fledging MCP with the composition of the total study area.	To investigate whether song thrushes feeding fledglings utilise the habitat available to them randomly. Also to see if there are changes in the foraging and post-fledging MCP.

3.4 Results

3.4.1 Habitat use by breeding birds

3.4.1.1 Skylarks

A total of 70 nests were found during the study period (26 in 2000, 30 in 2001 and 14 in 2002). Compositional analysis showed that habitats within 118m of nests differed significantly from random with respect to availability (Wilk's lambda = 0.096, $F_{(8, 62)} = 72.745$, $P < 0.001$), and there was no significant difference between years (Wilk's lambda = 0.857, $F_{(8, 61)} = 1.274$, $P = 0.274$). Habitat ranking by breeding skylarks was:

BB >>> CSA > Cereal > Othcropsa > GRSA > KSA > Other_veg >>> BLCrop >>>> Other.

These results showed that beetle banks were significantly more common near nests relative to their availability than any other habitat. Broadleaved crops and 'other' habitats ranked lowest relative to their availability (Chapter 3, Appendix 3, Table a) and were significantly less common around nests than all other habitat types.

3.4.1.2 Yellowhammers

A total of 35 nests were found during the breeding season of 2000. Compositional analysis showed that habitats within 191m of nests differed significantly from random across the study site with respect to availability (Wilk's lambda = 0.213, $F_{(8,27)} = 12.504$, $P < 0.001$). Habitat ranking for area of habitats found around yellowhammer nests was:

Cereal > BB = Other veg > KSA > CSA > BLCrop > Othcropsa > Other > GRSA.

Cereal, beetle banks, 'other vegetation', kale set-side and cereal set-aside were more common around the nest site than would be expected relative to their availability. Beetle banks, cereal crops, kale set-aside and other

vegetation were significantly more common within the nesting area than grass set-aside relative to their availability. Likewise beetle banks and other vegetation were significantly more common than 'other crop set-aside' than would be expected, and beetle banks, cereal crops, kale set-aside and other vegetation than 'other' habitats (Appendix 3, Table b).

3.4.1.3 Song thrushes

A total of 297 nests were found during the three years (51 in 2000, 126 in 2001 and 120 in 2002). Of these 65 had already failed or successfully fledged young. All nests found were included in this analysis. A radius of 118m was drawn around each nest, which related to the 95th percentile area of foraging MCP areas.

Year had a significant effect on habitats surrounding song thrush nests (Wilk's lambda = 0.819, $F_{(9, 287)} = 7.035$, $P < 0.001$). Therefore compositional analysis was carried out on each year separately. This showed that habitat within 118m of nests differed significantly from random with respect to availability across the study site for each year (2000 - Wilk's lambda = 0.087, $F_{(9, 42)} = 48.682$, $P < 0.001$, 2001 - Wilk's lambda = 0.139, $F_{(9, 117)} = 80.414$, $P < 0.001$, 2002 - Wilk's lambda = 0.089, $F_{(9, 111)} = 126.005$, $P < 0.001$). Simplified rankings for relative habitat use are given below.

2000 Bound > Herb veg > Wood > Other > Grass veg > Garden > Cereal > Allsa > BLCrop > PP

2001 Wood > Bound > Other > Herb veg >> Grass veg >> Garden > BLCrop >> Allsa > PP > Cereal

2002 Wood >>>> Herb veg > Bound > Other >>>> Garden > Cereal > Grass veg >> Allsa > PP >>>>
BLCrop.

Wood, boundary, 'other' and herbaceous vegetation were consistently more common near to nests relative to their availability across the study site. Permanent pasture, all set-aside and broadleaved crops are consistently the least common habitats relative to their availability around nest sites.

3.4.2 Habitat use by foraging birds

A total of 35 skylark (13 in 2000, 15 in 2001 and 7 in 2002), 16 yellowhammer and 22 song thrush (2 in 2000, 12 in 2001 and 8 in 2002) nests were involved in foraging watches over the course of the study.

3.4.2.1 Skylarks

Data were analysed from 35 nests using all known foraging sorties within the 95th percentile distance (797 from 838 in 86 watches) from each nest (mean per watch $\pm 1\text{SE} = 9.74 \pm 0.61$). The maximum foraging distance observed in any year was 299m, and 50% of all foraging sorties were less than 39m from the nest (Table 5).

Table 5: Skylark foraging distance (m) differences between years and the number of foraging sorties recorded (n).

Year	Average distance travelled (m)				
	100th percentile N	99th percentile	97th percentile	95th percentile	50th percentile
2000	298.7	280289.3	175.5	146.5	33.6
2001	226.4	358184.4	120.4	110.7	44.5
2002	190.6	200156	143.95	126.35	43.59
All years	298.7	838190.6	151.2	118.3	39.33

At the nest level (foraging locations vs foraging circle)

Due to several missing available habitats the 9 habitat groups were further combined to 7. Managed set-aside included CSA + Othcropsa + KSA. There was no significant difference in habitat use between years (weighted mean Wilk's lambda = 0.428, $P = 0.537$, by randomisation) but skylark foraging habitat use differed significantly from random with respect to habitat availability around the nest (weighted mean Wilk's lambda = 0.1195, $P < 0.001$, by randomisation).

Habitat ranking across the three years was:

Mansa >>> BB = GRSA = Cereal > BLCrop >> Other_veg > Other

Managed set-aside was used significantly more than all other habitats, relative to its availability (Figure 3, Appendix 3, Table c) as a foraging habitat whilst provisioning nestlings. 'Other vegetation' and 'other' habitats were used significantly less than expected than all other habitats. Skylarks were never seen to forage in 'other' or 'other vegetation'.

At the study site level (foraging circle vs area study site)

The compositions of foraging habitats around the nest whilst provisioning young, within the 118m radius, were compared with the composition of available habitats across the study site. There was no significant difference in skylark foraging range composition between years (Wilk's lambda = 0.806, $F_{(8, 26)} = 0.785$, $P = 0.620$) and skylark habitat composition within the radius was not random, i.e with respect to habitat availability across the study site (Wilk's lambda = 0.073, $F_{(8, 26)} = 42.555$, $P < 0.001$). Habitat ranking was:

BB >>> CSA > Othcropsa > Cereal > GRSA >> Other veg > KSA > BLCrop >> Other

Beetle banks ranked first and were significantly more common around nests than any other available habitat, followed by cereal set-aside, other crop set-aside, cereal and grass set-aside (Appendix 3, Table d). These habitats were used significantly more than other vegetation, kale set-aside and broadleaved crops, which were used significantly more than 'other' to form the foraging area around the nest. Skylarks utilised 'other' and 'other vegetation' less than would be expected relative to their availability on the study site (Figure 3).

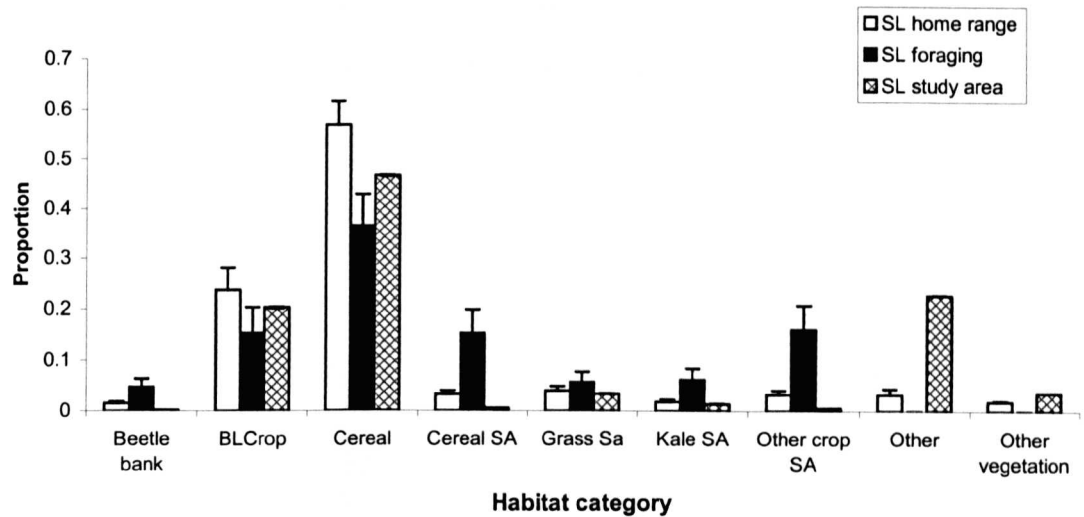


Figure 3: Mean habitat availability and habitat use by provisioning skylarks across Loddington farm estate, \pm 1SE, during 2000-2002.

3.4.2.2 Yellowhammers

At the nest level (foraging locations vs foraging circle)

Due to several missing available habitats the 9 habitat groups were further combined to 7. ‘BB+GRSA’ included beetle banks and grass set-aside and ‘Cropsa’ included cereal set-aside and other crop set-aside. Data from 16 nests, 37 watches, in 2000 were analysed using all known foraging sorties within the 95th percentile distance (191m) from each nest (mean per watch \pm 1SE = 7.03, \pm 1.056). The foraging range observed was 2.7 - 400m and 50% of all foraging sorties were less than 60 m from the nest.

Compositional analysis showed a significant difference in habitat use within the foraging range, (weighted mean Wilk’s lambda = 0.035, $P = 0.001$, by randomisation). Habitat ranking for yellowhammers was:

Cereal > BB+GRSA > Cropsa > BLCrop > KSA > Other_veg > Other

Cereals were the highest-ranking foraging habitat followed by beetle banks+grass set-aside and crop set-aside. Cereals were used significantly more than kale set-aside, ‘other’ and other vegetation relative to availability. ‘Other’ habitats and ‘other vegetation’ were utilised less than all other habitats relative to availability (Figure 4, Appendix 3, Table e).

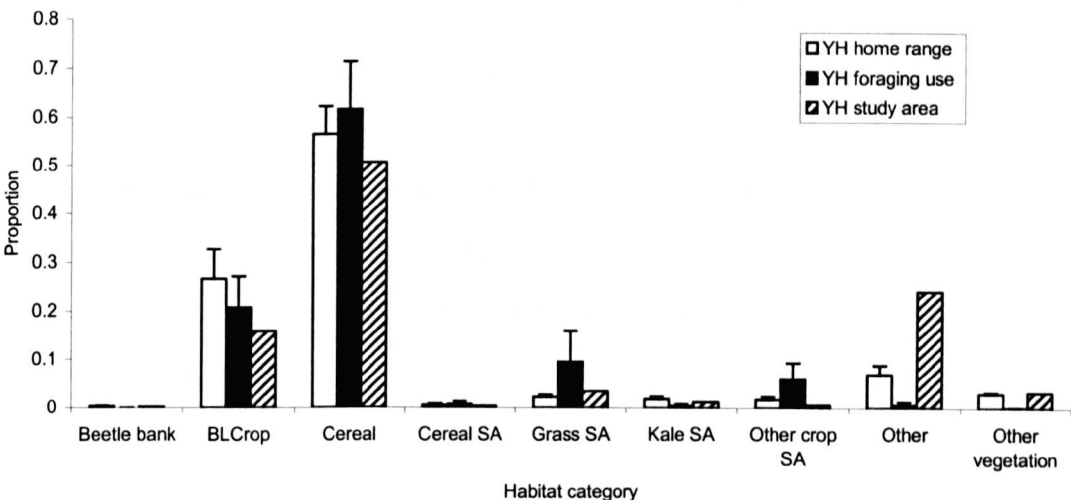


Figure 4: Mean habitat availability and habitat use by provisioning yellowhammers across Loddington farm estate, \pm 1 SE, during 2000.

At the study site level (foraging circle vs area study site)

Compositional analysis showed a significant difference in habitat use at this level by yellowhammers (Wilk’s $\lambda = 0.036$, $F_{(8,8)} = 27.138$, $P < 0.001$). Yellowhammers used broadleaved crops and cereal crops relatively more than would be expected from their availability and ‘other’ less than would be expected (Figure 4).

Habitat ranking for yellowhammers was:

BB > Cereal > Othcropla > Other veg > CSA > KSA > GRSA > BLCrop > Other

Beetle banks, cereal, cereal set-aside, other crop set-aside and other vegetation were used significantly more than 'other', and cereals, other crop set-aside and 'other vegetation' were used significantly more than grass set-aside (Appendix 3, Table f).

3.4.2.3 Comparison of skylarks and yellowhammers in 2000

At the nest level (foraging locations vs foraging circle)

Habitat groups cereal set-aside and other crop set-aside were combined to form 'crop set-aside' because only 30% of nests involved in the analysis contained both set-aside types around the nest, leaving many missing available habitat values. BB and GRSA were also combined due to several missing available values, reducing the habitat categories from 9 to 7.

There was a significant difference in relative use of habitats between species (weighted mean Wilk's lambda = 0.334, $P = 0.026$, by randomisation). This difference was mainly due to differential use of cereals, kale set-aside and other-veg (see rankings, Appendix 3, Table g). Therefore each species data set was analysed separately. Single species compositional analysis showed a significant difference in habitat use by skylarks in 2000 (weighted Wilk's lambda = 0.054, $P = 0.004$, by randomisation).

Habitat ranking for skylarks was

KSA > Cropsa > Cereal > BB+GRSA > Other > BLCrop > Other_veg

Yellowhammers also showed a significant difference in their habitat use within their foraging range in 2000 (weighted Wilk's lambda = 0.035, $P = 0.001$, by randomisation). See sub-section 3.4.2.2 for habitat ranking.

Cereals, which ranked first for yellowhammers, were used proportionally more than expected by yellowhammers and less than expected by skylarks (Figure 4). Kale set-aside was used more for foraging by skylarks and less by yellowhammers, despite their foraging ranges encompassing similar proportions (Figure 4). This habitat type ranked first for skylarks and fifth for yellowhammers. Skylarks used crop set-aside

proportionally more for foraging than yellowhammers, encompassing more of it within their foraging range. This habitat ranked second for skylarks and third for yellowhammers. The foraging range of yellowhammers contained proportionally more broadleaved crops than skylarks, but both species utilised it less than would be expected relative to its availability (Figure 5). Skylarks never utilised ‘other_veg’ for foraging, accounting for differences in habitat use by the two species.

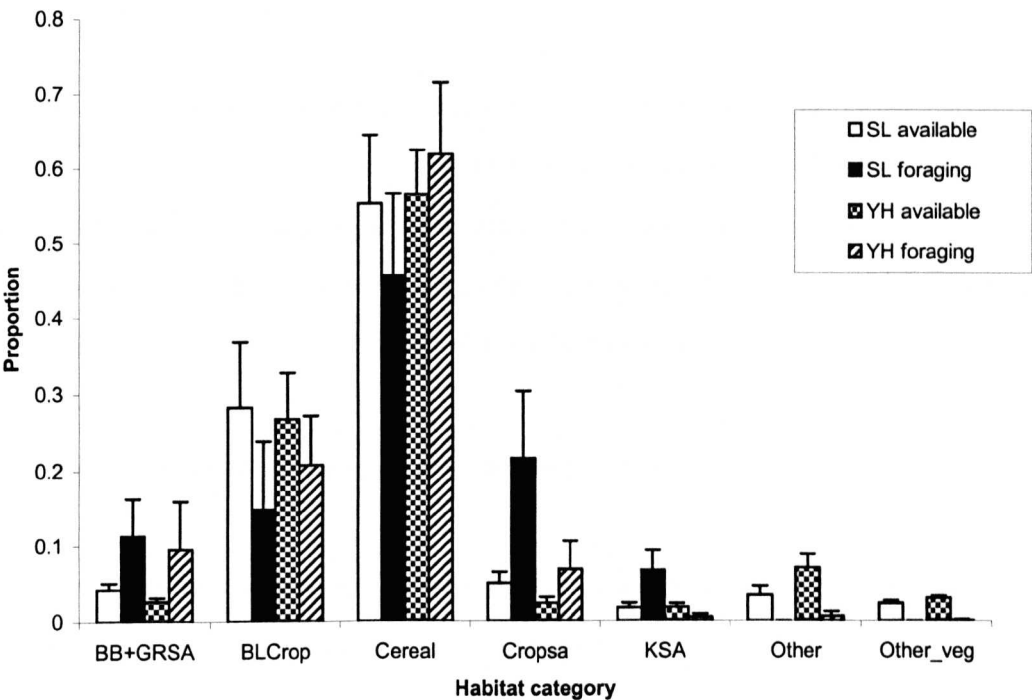


Figure 5: Mean habitat availability and habitat use (i.e. for foraging) by provisioning skylarks and yellowhammers across Loddington farm estate, ± 1 SE, during 2000.

3.4.2.4 Song thrushes

At the nest level (foraging triangles vs MCP foraging range)

Broadleaved crop and garden habitats were excluded from the analysis due to several missing available habitat values (following Aebischer et al., 1993).

There was no significant difference in habitat use between years (weighted mean Wilk's lambda = 0.370, $P = 0.932$, by randomisation). Compositional analysis showed a significant difference in habitat use within the foraging range (weighted mean Wilk's lambda = 0.225, $P = 0.054$ by randomisation).

The simplified ranking of song thrush foraging habitats whilst provisioning nestlings (also see Appendix 3, Table h) was

Wood > Other > Bound >> Grass_veg = Herb_veg > Allsa = PP > Cereal

Woodland was the most used foraging habitat relative to availability within the foraging MCP. Permanent pasture, cereals, broadleaved crops and all set-aside were used less than expected when song thrushes were provisioning nestlings and boundary habitats, gardens, 'other' and herbaceous vegetation used more (Figure 6). Provisioning song thrushes used wood significantly more than all set-aside and cereal, and 'other' and boundary habitats significantly more than grass vegetation (Appendix 3, Table h).

At the study site level (MCP foraging range vs total study area)

The MCPs of 22 nests were included in this analysis across the three years. There was no significant difference in habitat use between years (Wilk's lambda = 0.705, $F_{(9,12)} = 0.557$, $P = 0.807$) but song thrush habitat use differed significantly from random with respect to availability around the MCP foraging range (Wilk's lambda = 0.081, $F_{(9,13)} = 16.397$, $P < 0.001$).

Single sample t-tests were carried out on each log-ratio difference to identify which habitats were used the most (Appendix 3, Table i). A simplified ranking of results showed that woodland, 'other', herbaceous vegetation and boundaries were the most used habitats by foraging birds with respect to availability. Wood was used significantly more than all other habitat categories apart from boundaries, herbaceous vegetation and 'other' habitats. Herbaceous vegetation was used significantly more than all other habitat categories apart from boundaries, gardens and grass vegetation. 'Other' was used significantly more than all other habitat categories apart from wood, boundaries and herbaceous vegetation. Permanent pasture, broadleaved crops and cereals were least used relative to availability by foraging birds.

Wood > Other > Herb veg > Bound > Grass veg > Garden > Allsa > PP > BLCrop > Cereal

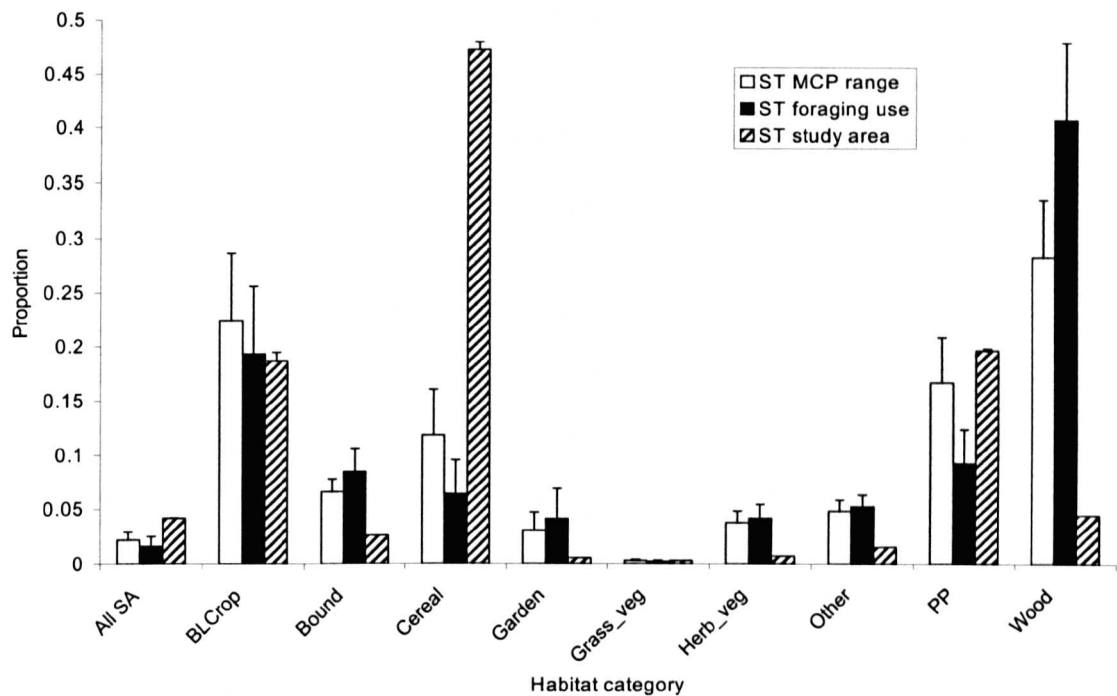


Figure 6: Mean habitat availability and habitat use by provisioning song thrushes across Loddington farm estate, \pm 1 SE, during 2000 - 2002. MCP established using outer vertices of error triangles. Habitat use established using the composition of habitats within the provisioning triangles.

3.4.2.5 Habitat use by song thrush post fledging

No analysis was carried out at the nest site level because only an additional 10 fixes were collected for the post-fledgling period. No detailed comparison could therefore be made between song thrush habitat use when provisioning nestlings or dependent fledglings but analysis was carried out to see if the foraging range expanded once chicks left the nest.

At the study site level (Post fledging MCP vs total study area)

Paired t-tests showed that there was a significant difference in MCP areas between the provisioning stage and post fledging stage, $t = 3.88$, $P = 0.002$, $df = 14$, $n = 15$ (number of nests involved in the analysis). The mean provisioning MCP was 1.73ha ($n = 15$) and the mean post fledging MCP was 2.62ha ($n = 15$). When the only bird from 2000 with post-fledging data was excluded from the analysis the difference was still significant, $t = -3.56$, $P = 0.004$, $df = 13$ (mean provisioning MCP 1.75 ha and mean post-fledging MCP 2.54 ha, $n = 14$).

Fifteen sets of post fledging data were used in the analysis. Compositional analysis showed that there was no difference in habitat use between years (Wilk's lambda = 0.459, $F_{(9,5)} = 0.654$, $P = 0.727$) and habitat composition within the post fledging MCP was not random, with respect to availability across the study site (Wilk's lambda = 0.031, $F_{(9,6)} = 20.999$, $P = 0.001$). Ranking of song thrush foraging habitats post fledging chicks were:

Wood > Herb_veg > Other >> Bound > Grass_veg > Garden > PP > Allsa > Cereal > BLCrop.

Woodland was the most used habitat by song thrush post-fledging with respect to availability, followed by herbaceous vegetation and 'other' habitats. All set-aside, cereal and broadleaved crops were used least relative to availability post-fledging (Appendix 3, Table j). Woodland, herbaceous vegetation and 'other' habitats were used significantly more than all other habitat types relative to availability post fledging. Figure 7 shows that song thrushes with nestlings utilise woodland, 'other', herbaceous vegetation and boundary habitats more than when young have fledged. The post-fledging MCP incorporates more open habitats such as broadleaved crops, cereals, permanent pasture and gardens than the provisioning MCP.

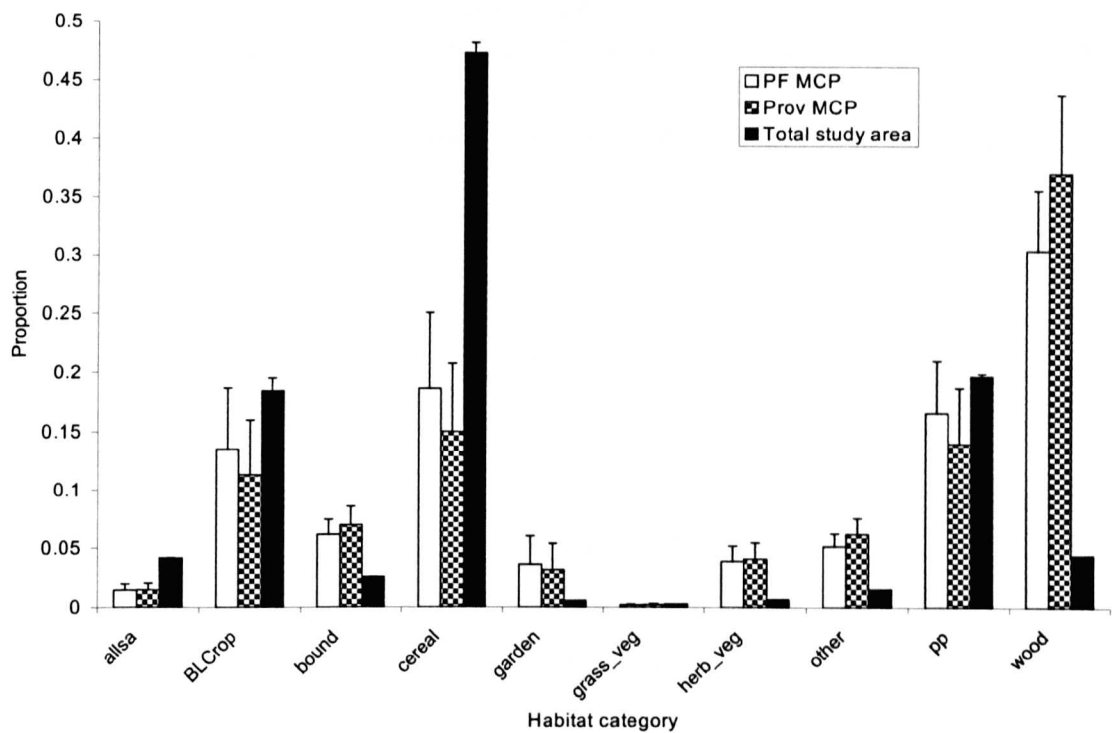


Figure 7: Mean habitat availability and habitat use by song thrushes during the provisioning and post-fledging stage, across Loddington farm estate, \pm 1SE, during 2000 - 2001.

3.4.2.6 Song thrush home range estimates

Home range sizes (of non-nesting birds) were larger than song thrush provisioning and post fledging ranges (Table 6).

Table 6: Differences in song thrush home range, foraging minimum convex polygon (MCP) and post fledging (PF) MCP size, using MapInfo to calculate areas (ha). N = number of individuals. Size (ha) changes with fix number.

Home range sizes	Mean home range (ha)	N	Mean foraging MCP	N	Mean PF MCP	N
<i>All birds</i>	3.330 ± 1.180	9	1.891 ± 0.265	22	2.623 ± 0.461	15
<i>Males only</i>	3.710 ± 1.454	7	2.006 ± 0.274	20	2.711 ± 0.492	13
<i>Females only</i>	2.035 ± 1.898	2	0.912 ± 0.651	2	2.051 ± 1.741	2
<i>All bird with 20+ fixes</i>	4.070 ± 1.403	7	1.774 ± 0.274	19	-	-
<i>Males only with 20+ fixes</i>	4.090 ± 1.660	6	1.923 ± 0.283	17	-	-
<i>Males in 2001 only</i>	2.370 ± 0.678	6	2.381 ± 0.459	11	2.898 ± 0.833	7
<i>Males in 2001 with 20+ fixes</i>	2.560 ± 0.796	5	2.385 ± 0.546	8	-	-
<i>Males in 2002 only</i>	-	-	1.546 ± 0.180	8	2.493 ± 0.520	6

3.5 Discussion

3.5.1 General behaviour

Female skylarks arrive on the breeding site after the males have set up territories, often returning to their previous territory and partner (Delius, 1965). Under the close guard of the male, the female chooses the nest location, builds the nest and incubates the eggs. Both parents feed the nestlings but during this study it was observed that the female undertook most of the provisioning of nestlings particularly when they were older. Female yellowhammers also join territorial males (Andrew, 1956) and choose the nest site within the territory. The female is solely responsible for incubation but the male assists in feeding the young (Sundberg, 1992). However it was apparent from observations during the current study that the female carried out most of the nestling provisioning whilst the male either sang close to the nest or was out of sight. Like the skylark and yellowhammer, the female song thrush also builds the nest and incubates the eggs. In contrast to the other two species, the female song thrush broods her chicks tightly, whilst the male is the main food provider until the

chicks are at least 8 days old. The male song thrush has also been reported to feed the female whilst she is on the nest (Hartley, 1967).

In summary: For skylark and yellowhammer, it is the female who has most influence on habitat use during the breeding season whereas for the song thrush it appears to be the male.

3.5.2 Habitat use by breeding and provisioning birds

When examining habitat use by breeding birds, all nests found were included in the analysis. For provisioning birds, it should be remembered that data could only be collected from nests that survived both the laying and incubation stage. It is likely, although this would be difficult to determine, that nests that survived through to the nestling stage experienced a lower likelihood of predation, an important cause of skylark, yellowhammer and song thrush nest failure (Chapter 2). Nests were scored on their exposure and this proved not to influence nest survival rates, although habitats around the nest could potentially influence survival (Chapter 2). Another caveat to consider was that dominant neighbours of the same or different species might have influenced habitat selection, although this aspect was not examined within this thesis.

3.5.2.1 Skylarks

The results of this study show that breeding females did not position their nests randomly across the farm, nor did they forage randomly within habitats around the nest. The importance of cereals and set-aside, whether cereal or non-crop based, to nesting skylarks was emphasised and the avoidance of broadleaved crops and habitats incorporating woodland, buildings, hedgerows and ditches highlighted. These findings are supported by results documented in Chapter 2, where skylark nest densities were generally highest in set-aside and lowest in broadleaved crops. Skylarks collecting food for nestlings used all types of set-aside more often than would be expected, relative to their availability, within 118m of the nest. Cereals ranked higher than expected as a favoured foraging habitat relative to availability (Figure 2), although they did comprise 45% of the available habitat. Analysis did not test for a seasonal effect and it is likely they would be used less as the season progresses, as the crop grows denser, both to nest and forage in (Schlöpfer, 1988; Eraud & Boutin, 2002). This could be partly due to their inferior invertebrate resources compared to non-cropped habitat types,

such as set-aside (Moreby & Aebischer, 1992) and field margins (Thomas & Marshall, 1999). Many passerine species have been shown to select cereals less for foraging than would be expected when feeding nestlings with a predominantly invertebrate diet (Stoate et al., 1998; Brickle et al., 2000; Whittingham et al., 2001; Wilson, 2001; Morris et al., 2001a). The relatively high ranking of cereals during nesting could be an artefact of most set-aside habitats at Loddington being situated within cereal fields, although many nests were located in cereals.

Beetle banks, in particular, were found to be significantly more common around skylark nests compared to all other habitat types and were an important foraging habitat type for provisioning birds. They harbour overwintering predatory arthropods, which move into the crop during the summer and help control aphids, hence providing a potential chick food source (Thomas et al., 1991; Collins et al., 2003). They also offer sheltering grounds to mammals, birds and invertebrates and often provide nest sites. Provisioning birds were frequently observed pushing their way into the vegetation to forage. Beetle banks made up an extremely small proportion of the landscape available (0.25%), serving to break up an otherwise homogeneous land cover within a large arable field and consequently increase habitat diversity within a territory. Skylarks therefore showed a clear habitat selection when establishing nest sites near to beetle banks.

All types of set-aside (particularly managed set-aside) emerged as important foraging grounds for provisioning skylarks, supporting work by Poulsen et al. (1998) and Wilson (2001). Most set-aside strips at Loddington are sown with Wild Bird Cover, containing cereal or kale-based mixtures (see Boatman & Bence, 2000), and were used significantly more than any other habitat category. Cereal based set-aside types (sown with wheat or triticale) generally offer the same habitat structure as a cereal crop but with greater sward heterogeneity, greater plant species diversity (hence more potential chick food invertebrates) and shelter whilst foraging on the ground from potential visual predators. The association of skylark territories with set-aside has previously been recorded at Loddington (Boatman & Stoate, 2000; Boatman et al., 2000). One of the explanations for the selection of set-aside by provisioning birds is that these habitats receive restricted fertiliser input and no insecticides or fungicides, hence increasing the abundance of potential chick food invertebrates (Wilson et al., 1995). In addition, the sward structure is more heterogeneous than winter sown cereal crops so may offer easier access and manoeuvrability within the habitat. These factors are further investigated in Chapter 4.

During the three-year study the majority of set-aside was non-rotational and positioned across the farm in strips, either within the centre of the field or along hedgerows. Cereal and kale set-aside strips or grass tracks flanked beetle banks, or they bordered the crop edge on at least one side. The importance of the positioning of beetle banks and other set-aside for nesting and provisioning skylarks is emphasised in this study, particularly as set-aside strips rather than blocks of set-aside benefit many territories (Sotherton et al., 1994). Other studies consistently report the importance of set-aside during the breeding season for nesting and foraging (Henderson & Evans, 2000; Vickery & Buckingham, 2001; Donald et al., 2001b; Vickery et al., 2002; Firbank et al., 2003). Donald (1999) suggested that on lowland farmland today the skylark breeding season could be lengthened if territories contained more than two habitats with differing crop structure throughout the season (as shown by Schläpfer (1988) in Switzerland). The set-aside laid out in strips of adjacent habitat types, with their heterogeneous structure, serves to fulfil this purpose at Loddington.

Broadleaved crops and 'other' habitats (consisting of woodland, hedges and buildings etc) were used significantly less than would be expected relative to their availability around skylark nests and for foraging. This result is unsurprising, since it is probable the structure and fast growing nature of broadleaved crops, namely oilseed rape or beans, renders these crops unsuitable as either a nesting or foraging site as the season progresses. Skylarks are also known to avoid boundary features (Buckingham, 2001) such as hedges and ditches and association with man, and these habitats were generally avoided around nest sites and within foraging ranges.

In 2000 and 2001, 26 and 30 nests (respectively) were found. However in 2002, only 14 nests were found across the whole of the breeding season. Surprisingly, considering that in previous years set-aside had been an important nesting habitat (see Chapter 2), nearly all nests in 2002 were found in cereal crops and only one on grass set-aside. In 2002, cereal crops appeared to grow more uniformly than in the previous years, with relatively few patches caused by water-logging or hare (*Lepus capensis*)/pigeon (*Columba palumbus*) damage. Game cover crops, in 2002, were generally densely sown, cereal-based with very little kale. As a result, by June (the peak-breeding season) there was relatively little bare ground, leaving insufficient room for nesting. This may account for cereals ranking higher than expected for use by provisioning birds. Another peculiarity was that male singing activity stopped in early June and very little further breeding activity was detected on

the farm. This suggests that skylarks finished their breeding season early and abandoned territories due to habitat structure limiting the breeding season, as suggested might happen by Donald (1999).

In summary: set-aside strips at Loddington were preferred habitats for breeding skylarks to nest and forage in. However, most farms do not present set-aside in strips across cereal fields, but rather in blocks, so these results do not generalise readily to other farms. The results of this chapter provide support for the hypothesis that skylarks use wildlife crops and semi-natural habitats more than commercial crops relative to their availability when provisioning young. Cereal crops were however shown to be important for nesting and foraging during the breeding season.

3.5.2.2 Yellowhammers

The results of this study demonstrate that yellowhammers did not position their nests or forage randomly across the farm with respect to habitat availability, and emphasised the importance of cereal-based set-aside and cereal crops to provisioning yellowhammers. Cereal crops were more commonly found around the nest than other habitat categories. In addition to this, cereal crops and cereal based set-aside were important habitats within the yellowhammer foraging range around the nest and as a foraging habitat. Kyrkos et al. (1998) suggested there might be a critical area of cereal required to maintain yellowhammer territory density and results from the present study lend some support to this.

Breeding yellowhammers have been closely associated with cereal crops in several other studies, through the establishment of territories or as a foraging habitat (Biber, 1993c; Stoate et al., 1998; Kyrkos et al., 1998; Bradbury & Stoate, 2000; MacCleod, 2001; Morris et al., 2001a; Perkins et al., 2002). Stoate et al. (1998) demonstrated a change in cereal crop use from winter barley early in the breeding season to winter wheat later in the breeding season as the crop ripened in Leicestershire. MacCleod (2001) showed provisioning yellowhammer preference for cereals and game cover crops in Scotland. Cereal crops and set-aside sown with cereals also provide yellowhammers with ripening grain as a food source as the season progresses, which is utilised after the last week in June for nestlings (Stoate et al., 1998), despite it possibly being a sub-optimal food source when invertebrates are unavailable (Watson, 1992).

In contrast to this research, numerous studies have recorded an association between foraging yellowhammers and field margins, verges and grass habitats (Stoate & Szczur, 1997; Bradbury et al., 2000; MacCleod, 2001; Morris et al., 2001a; Perkins et al., 2002; Vickery et al., 2002), probably because of the large number of invertebrates associated with such habitats compared to cultivated fields (Dennis et al., 1994; Thomas et al., 2001). However, in the current study these habitats were used less than would be expected due to their availability and were infrequently observed being used by adults feeding nestlings. 'Grass set-aside+beetle banks' at the nest level ranked highly for provisioning yellowhammers (see 3.4.2.2). Observations showed grass set-aside was the main foraging ground out of the two habitats. Possibly this may be because yellowhammers do not like to forage in the centre of the field in a beetle bank but would along crop or track edges in suitable grass habitats (if both grass set-aside and beetle banks are similar in structure and vegetation). Although yellowhammers were never observed foraging within beetle banks alone, despite them being present in most foraging ranges, they emerged as an important habitat at the study site level, i.e. the foraging area around the nest, perhaps because cereal crops or another crop set-aside strip flanked beetle banks. Invertebrates would cross from the beetle bank into the other habitats mentioned, thus creating good foraging grounds (Thomas et al., 1991; Collins et al., 2003). Beetle banks were also similar in structure to grass margins around field or track edges, which are also known to harbour predatory arthropods that disperse into the crops (Coombes & Sotherton, 1986). Most types of set-aside, except grass set-aside, were more common around the nest site relative to availability, probably because set-aside is likely to support an abundance of important chick food invertebrates compared to cereals (Moreby & Aebischer, 1992; Poulsen et al., 1998; Henderson et al., 2000a; Henderson et al., 2000b).

Findings from this study showed that the 'other' habitat category, which included permanent pasture, hedgerows, woodland and buildings, was consistently one of the lowest ranking habitats used across all levels of analysis. The close association of yellowhammers with hedgerows (Morgan & O'Connor, 1980) was therefore swamped by the other habitat types included in this category. Grassland habitats were also avoided in studies carried out by Bradbury et al. (2000), MacCleod (2001) and Morris et al. (2001a) in the breeding season. At Loddington this could be due to grazing pressure from sheep, reducing heterogeneity in sward structure and possibly causing a decline in suitable invertebrate food abundance. In addition to this, most yellowhammer territories were situated away from permanent pasture and buildings (pers.obs). This could

account for their low ranking habitat use, although in winter the reverse may be true. Perkins et al. (2000) showed that yellowhammers were found significantly more frequently in grass fields next to buildings in winter and suggested that since yellowhammers are grain feeders they are therefore associated with farm buildings where livestock are fed or grain is stored (O'Connor & Shrubbs, 1986). Before agricultural intensification, yellowhammers selected pasture and meadows over arable crops (Wild, 1938), so the intensification of grassland management is implicated in the decline in use of this habitat type (see Bradbury & Stoate, 2000).

In the current study of provisioning yellowhammers, birds generally foraged within 80m of the nest, utilising reliable food sources close to the nest without having to fly longer distances. The average foraging flight distance in this study was shorter than that of MacCleod (2001), who recorded a mean distance of 55m at Gilston and 115m at Memus, Scotland, although it was rare in both studies for individuals to consistently travel the maximum-recorded flight distance. Invertebrate abundance is known to decrease with distance into the crop from field margins and boundaries (Thomas et al., 1991; Moreby & Aebischer, 1992). Since yellowhammers are closely tied to nests within field boundaries and margins, they are less likely to travel extended distances if their foraging requirements are met closer to the nest (Vickery & Fuller, 1998; MacCleod, 2001; Morris et al., 2001a; Perkins et al., 2002; Vickery et al., 2002). The costs to individual provisioning adults are likely to be reduced when travelling shorter foraging distances to food rich areas, and could also reduce predation risk (Chamberlain et al., 1999c).

Beans and oilseed rape were generally not selected as foraging habitats or around the nest. Stoate et al. (1998) suggest it is the thick canopy of well-established oilseed rape that makes it largely impenetrable by the time that chicks are in the nest. However, direct observation during the current study showed that yellowhammers would forage within the field edges or land within sparse patches of the crop, created by water logging or pigeon damage, enabling them to forage on more open ground even when crops were fully grown. MacCleod (2001) and Morris et al. (2001a) found that yellowhammers selected oilseed rape more when adjacent to the nest, as it supported a high number of coleoptera (MacCleod, 2001).

In summary: yellowhammers utilised non-crop habitats and semi-natural habitats more than would be expected relative to their availability, but cereal crops and set-aside sown with cereals were of particular importance to this species at Loddington. The yellowhammer would benefit from the maintenance of field margin habitats, beetle banks and cereal-based set-aside sown in strips across cereal fields and also the management of cereal crops.

3.5.2.3 Skylarks and yellowhammers

Compositional analysis confirmed that skylarks and yellowhammers utilised available foraging habitats differently. The main differences between species was in the use of cereals, used more by yellowhammers and less by skylarks, and kale set-aside, used more by skylarks and less by yellowhammers relative to availability. Skylarks also never foraged in 'other vegetation'. However, the foraging range of yellowhammers was almost twice the size of skylarks. Differences between species therefore have to be interpreted with caution as area effects are confounded with species. Set-aside, generally under Wild Bird Crop management (cereal or kale-based mixtures) and grassy habitats (beetle banks and grass set-aside) emerged as important foraging habitats to both species in 2000.

The results of this study suggest that both species would benefit from habitat management of non-rotational set-aside sown in strips across cereal fields, such as the provision of game bird cover strips and both cereal and kale based set-aside. Cereal crop management and grass tracks and beetle banks are also likely to benefit each species. Skylarks would not benefit from habitat management near to field boundaries (as yellowhammers would) but carefully placed set-aside, within their approximate foraging ranges of 150m and 200m respectively, could be beneficial to both.

3.5.2.4 Song thrushes

The results of this study demonstrate that breeding song thrushes do not position their nests or forage randomly across the farm with respect to habitat availability. These results emphasise the importance of woodland, boundary, herbaceous and grass vegetation habitats to both nesting and provisioning song thrushes,

similar to Peach et al. (2004). In addition to these, arable crops, permanent pasture and set-aside were consistently avoided, both when establishing the nest and when foraging for nestlings. Peach et al. (2004) also found cereals were avoided by provisioning song thrushes in their mixed study site in Sussex.

Selection of woodland and boundary habitats at the nest and study site level highlights the importance of nesting cover for song thrushes. Most nests within territories associated with woodland were generally sited along the edges rather than within the centre (pers.obs), as found by Mason (2001) and Peach et al. (2004). Results from Chapter 2 showed that nests were most frequently built in woodlands and boundary habitats, which further illustrates the importance of these habitats to this species. Habitat selection around song thrush nests changed across the three-year study period. Boundary habitats, such as hedgerows and ditches, were more common around nests relative to availability in 2000, followed by herbaceous vegetation and woodland. This could be partly due to the fact that only a sub-sample of nests were located in 2000, being the year of the pilot study. In the following two years woodlands were consistently more common next to nests than would be expected relative to availability. Roads and buildings (contained within 'other' habitat category) were often situated adjacent to woodland and boundary habitats, which could account for them ranking fairly highly both for nesting and provisioning birds. Management of the selected habitats appeared to benefit song thrushes at Loddington and nests in adjacent territories were sometimes found less than 15m apart. This is also reflected in the number of territories found on the study site, which increased from 14 in 1992 to 64 in 2001 (Stoate and Leake, 2001), although other factors such as predator control or winter food may have also influenced this.

Set-aside was used relatively less than would be expected with respect to availability by nesting females or provisioning adults, despite some bordering hedges or woodland. A study by Buckingham et al. (1999) suggests that set-aside is little used by song thrushes in winter, which is similar to the findings of this study in the summer, although Stoate et al. (2003, 2004) reported song thrushes to use kale-based Wild Bird Cover or set-aside in the winter. Despite broadleaved crops being little used by provisioning adults in this study, this habitat may be important to song thrushes in the winter (Wilson et al., 1996; Buckingham et al., 1999; Henderson & Evans, 2000). More unexpectedly, permanent pasture was consistently one of the lowest ranking habitat types and was less common than would be expected around the nest relative to its availability, despite it probably being a good foraging area (Tucker, 1992) and generally being bordered by hedgerows.

Peach et al. (2002, 2004) found, to the contrary, grazed grassland was an important foraging habitat for breeding song thrushes in a mixed farming landscape in Sussex but not on their arable farming landscape in Essex. On their mixed farming landscape song thrushes made more use of woodland and less use of gardens as the season progressed. The current study did not test for seasonal effects of habitat use because of sample size constraint, but few provisioning birds utilised gardens at Loddington, even though many tagged individuals had territories close to the village area and several breeding territories were situated around the village. The results from the current study are more comparable with Peach's mixed farming landscape, rather than the arable, although pasture was not used as much as expected relative to availability. This unexpected result could have been due to a number of reasons; the small sample size, a possible lack of suitable pasture around the nests of tagged birds, the fact it may have been a lesser quality feeding area compared to woodland and boundary habitats at the time the birds were being studied, it may have dried out quicker than other habitats decreasing the general availability of earthworms, it may have been too heavily grazed or simply due to lack of suitable foraging cover within that habitat type. The importance of gardens, hedgerows and woodland to breeding song thrushes on lowland farmland has been highlighted in previous studies (e.g. Sparks et al., 1996; Mason, 1998, 2000; Peach et al., 2004). Cereal fields were also strongly avoided by provisioning birds, as found by Peach et al. (2004), and this could be a reflection of the potentially lower earthworm availability within them (Tucker, 1992).

Woodland, boundary, other and herbaceous vegetation were consistently not only important habitats to adults when foraging for nestlings but also when provisioning dependent fledglings and their foraging range expanded. Hartley (1967) suggested that young song thrushes would remain in their parents' territory for a week and then disappear. However, using radio-telemetry, Hill (1998) showed that many young song thrushes dispersed over 100m from the nest up to seven days after fledging but did not move significantly further from the nest until independence. This may explain why Hartley (1967) did not see them after a week. Other studies show that young song thrushes and blackbirds remain in cover for the first two weeks out of the nest (Snow, 1955; Hartley, 1967; Simms, 1978) and this may influence habitat selection of foraging adults. Furthermore, song thrushes still utilised key foraging habitats that were more likely to remain damp, hence containing higher numbers of earthworms (Chamberlain et al., 1999c). The vegetation structure and canopy of these habitat types is likely to help retain moisture longer term, unlike cereals and, to a lesser extent, pasture.

Post-fledging fixes were taken two weeks after chicks left the nest and before they dispersed from the natal territory after 3 – 4 weeks (Hill, 1998). In the first week post-fledging most young song thrushes die as a result of natural causes. Those that survive the second week have a greater chance of reaching independence, probably because they can fly, escaping predation (Hill, 1998). In Hill's (1998) Dorset study of post-nestling mortality and dispersal of song thrushes and blackbirds, radio tags were used to recover dead young and predation was found to be the main cause of death of both dependent and newly independent thrushes. The current study made no concerted attempt to locate fledgling song thrushes before fixes were taken, so many of the adults tracked could potentially have lost all or some of their fledged brood. Consequently, post fledgling fixes may not be an accurate reflection of any change in adult foraging habitat use due to feeding fledglings. They may reflect, instead, a move to exploit the true home range area between nest attempts, or conversely they may be utilising habitats in which fledglings are hiding, even though it has been suggested that fledglings move to where their parents forage (Hill, 1998).

As a result of fledging chicks, parent birds may need to travel further from the nest to feed young, which may or may not stay together. Over the one to two week periods after leaving the nest, song thrush fledglings make the transition from being completely dependent on their parents for food to foraging for themselves. Independence would be reached between 21 and 35 days out of the nest, when they would leave the natal home range. As one would expect, the parent bird's foraging range expanded because of this. Song thrushes are known to make regular feeding visits beyond their territory boundary (Lack, 1966), but this study found that provisioning adults stayed within a more confined area when chicks had left the nest and were approaching independence. Hill (1998) found that dependent song thrush fledglings ranged over an area larger than the mean adult home range in March. By excluding triangles with more than 26 grid intersections in the current analysis, areas infrequently visited outside the normal foraging area by adults may have been excluded. Peach et al. (2004) found their global home range (all fixes from non-nesting birds) generally incorporated the nesting home range area (the area used by provisioning adults) and the current study also found non-nesting birds expanded their home range. In agreement with Peach et al. (2004) the current study found that female foraging ranges were smaller and closer to the nest than those of males, although sample size in this study was small.

In summary: at Loddington woodland and boundary habitats were heavily utilised by song thrushes both when nesting and foraging for nestlings and dependent fledglings. Permanent pasture, cereals and set-aside were generally avoided during the breeding season.

3.5.3 Limitations of the study

3.5.3.1 General

A caveat in trying to examine habitat availability to a breeding pair or across a study site requires boundaries to be set around a limited area. In doing this, the analysis assumes that all birds can utilise all habitats at liberty, which may not be the case with territorial species such as the skylark, yellowhammer and song thrush. Inter and intra-specific competition may affect habitat use (O'Connor & Shrubbs, 1986; Newton 1998). Therefore habitat availability may or may not truly represent what is genuinely available to each bird at the study site level but should not invalidate within-home-range comparisons (Aebischer et al., 1993). For the skylark and yellowhammer research, foraging habitat use was straightforward to define since birds were physically observed within different habitats. However, for song thrush, telemetry was employed as a tool to examine 'use' and established methods to determine MCPs had to be trusted and used (see section 3.5.3.2) due to the secretive nature of the species. One limitation of the analyses carried out was that distance of different habitat types from the nest was not taken into account, which may influence habitat use.

3.5.3.2 The use of telemetry for song thrush research

In order to obtain more precise habitat selection results, sample size (the number of tagged song thrushes) could have been increased. To compare utilised with available habitats Aebischer et al. (1993) recommend a sample size of 10, with an absolute minimum of 6, and preferably above 30. The lack of difference between use of habitats within the home range of non-nesting birds and study area could reflect small sample sizes or, more positively, could demonstrate that Loddington provides widely distributed habitats important to song thrushes across the breeding season. One of the limitations of this study was not being able to successfully catch song thrushes in mist-nets, similar to experiences of Hill (1998). A large amount of trapping time and

effort went into this part of the project for little return. Since the study was concentrating on foraging when provisioning young it was necessary to have nests that reached the nestling stage, past a few days old, and survived long enough to enable data to be collected. Adult birds also had to survive this period. To overcome this limitation, increasing trapping effort at more than one nest at a time with more trained people could have improved the catch rate. More females than males were caught but not tagged because, over the course of the study, it was found that females brooded chicks until they were over 9 days old. Taking fixes every 20 minutes from females on the nest would not have helped examine habitat use by provisioning adults, unless chicks were relatively old. However, tagged females may have been helpful in understanding changes in habitat use away from the nest once chicks had fledged, particularly if fixes were taken at random times across the day.

The times that fixes were collected covered a large part of a day in the life of the bird, except for the evening, so should be fairly representative of habitat use during the nestling period. One problem that was not so easily overcome was in the time delay between taking bearings (generally up to six minutes taken to complete a fix) due to only one person taking fixes. An effort to take fixes as quickly and efficiently as possible was made. For this project, the delay between bearings was also considered acceptable due to the fact that song thrushes spend several minutes on the ground foraging within the same habitat type before returning to the nest (pers.obs).

As birds were generally not seen foraging, the centre of the error triangle was not relied upon to determine fix position (see section 3.3.3.3). It was not considered an option to go in and find the foraging birds after each fix because it could have shifted the bird into another habitat type and also, more importantly, disrupted its natural foraging pattern whilst provisioning nestlings. If one fix was being taken three times daily, flushing the bird may have been an alternative to consider in order to validate fix positions when comparing them to the 'blind' fix. Alongside this is the error associated with each fix. The most accurate fix has at least a 10m² error associated with it, by plotting it with the methods used. This could mean that if a fix location fell on or near a boundary the fix location could be placed in one or the other habitat (i.e. in the boundary or the habitat next to it). Kenward (2001) suggested excluding fixes whose error covered more than one habitat. The mean number of habitats within all foraging error triangles was 2.39, \pm 0.16, $n = 22$ for this study. However for song

thrushes, which are known to forage on edge and boundary habitats, excluding fixes with more than one habitat was not an option since many of their locations would have been dropped. The results would not show whether they used habitat edges and habitat selection would have been severely biased. Peach et al. (2002) alleviated this problem by assigning any 10 m x 10 m square within their study sites that contained a boundary habitat to a boundary code. This resulted in over-estimating the true area of boundary habitat but was not considered to be a problem. White & Garrot (1990) also suggest designating an additional habitat category defined by any fix within a set distance from a habitat boundary.

Since large telemetry errors decrease efficiency and also bias measures of habitat use (Nams, 1989) this project used the error triangle itself as a measure of relative use, and as shown many of the triangles had small errors so habitat selection was considered to be quite accurate. White & Garrot (1990) suggest that triangulation may not be able to achieve the precision needed to detect habitat use, except in roughly defined habitats. Knowing that song thrushes use edge habitats, the habitat categories used in analysis were combined as broadly as possible to acknowledge this, but still maintain sufficient detail. The analysis of this study does not determine an exact foraging place within the error triangle but looks at habitat utilisation relative to availability by calculating the proportional habitat use for each triangle and averaging the proportions for each habitat across triangles to define use for each bird. This alleviates a bias towards particular habitats that may not be used. Peach et al. (2002) reported their error triangle was on average 0.048ha and 0.044ha on the Essex and Surrey sites. The current study had an average error triangle of 0.035ha, but did not attempt to suggest habitat use at a very fine scale. 0.035ha along a boundary edge could encompass about 6 different habitats, so if the centre of the triangle were not an accurate measure of where the bird was, results towards certain habitat types would be biased. The RSPB study (Peach et al., 2004) shows that woodland edges and wet ditches were preferred to dry ditches without hedges. With large error triangles (and possible fix 'position' inaccuracy of up to 30m) this should be a tentative suggestion. However they used a correlation approach to avoid bias, dividing home ranges into habitat parcels surrounding 'song thrush attractive' habitat features, such as field boundaries and woodland and tested for relationships between fix density and linked habitat composition using log-linear models.

In the current study, due to the methodology of collecting fixes over a three-hour period, bearings were taken from places known not to cross the flight path of the bird to the nest, or disturb it whilst foraging. As a result some of the error triangles were long and thin in nature rather than being more equilateral. Pinpointing the middle of triangle as a measure of where the bird was could have resulted in inaccuracies of habitat use. Observer error in this study is negligible because the author took over 95% of all fixes.

Another limitation of the post fledging habitat use study is that it provides an extreme snap shot in time rather than revealing any true foraging habitat changes because fixes were taken for one three hour period only, two weeks after fledging. Additional research could take this further and a series of adult fixes could be taken one, two and three weeks after chicks fledge to see if the MCP continues to increase in size and whether there are changes in habitat use. Searches to ensure chicks were alive would also have to take place, which would also provide information on whether chicks move to parental feeding areas as Hill (1998) suggests.

3.5.4 Conclusions

The results of this study confirmed that the skylark, yellowhammer and song thrush did not utilise available habitats for nesting or foraging randomly across the farm, reinforcing the findings of previous studies (Stoate & Szczur, 1997; MacCleod, 2001; Morris et al., 2001a; Peach et al., 2004). Set-aside, particularly beetle banks and kale or cereal-based mixtures under the Wild Bird Cover crop set-aside option, provided key habitats associated with breeding skylarks and yellowhammers, but was avoided by nesting song thrushes. However, woodland and boundary habitats, providing good nesting cover, were important habitats for breeding song thrushes.

Provisioning song thrushes also used woodland as a foraging habitat, which was avoided by the other two species, whereas provisioning skylark and yellowhammers heavily used set-aside when feeding nestlings. Both the yellowhammer and song thrush benefit from the maintenance of hedgerows and field boundaries in contrast to the skylark, which is known to avoid them. Many key foraging habitats for each species received less intensive management than arable crops, which may influence vegetation structure, invertebrate availability and movement (further examined in Chapter 4 and 5). However, results showed winter cereals

were utilised more than expected by provisioning skylarks and yellowhammers at the nest level, with cereals ranking first for provisioning yellowhammers. This may reflect nestling diet later in the season (Stoate et al., 1998).

Different aspects of available habitats, at the whole farm level, were shown to be important in different ways to each species. Variations in habitat availability and quality will dictate habitat preferences and will clearly vary between territories, farms and sites. The effects of habitat availability on the use of individual habitats means these results are specific to the characteristics of the site (Chamberlain & Crick, 1999) - Loddington, but highlight the need for a mosaic of habitat types across the farm level, supporting the views of Benton et al. (2003). Thus, it is likely that the on-going habitat management at Loddington has created better habitats within both the cropped and non-cropped environments that will benefit wildlife more than on farmland where no management has taken place. Agri-environment schemes and conservation management that will help benefit the study species and other bird species will be discussed fully in Chapter 7.

If food abundance determines foraging patterns (hence habitat use), it would be expected that provisioning birds select areas within preferred foraging habitats with higher abundance of chick food resources. If food abundance does not influence foraging patterns, accessibility to prey may play a role in determining where birds forage. The effects of vegetation structure and invertebrate abundance on provisioning birds are therefore investigated in the following chapter.

Appendix 3, Table a: Log ratio difference matrix for examining breeding *skylark* habitat use for nesting, 2000-2002, within a radius of 118m around the nest relative to habitat availability across the study site. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability. Log ratio difference = mean logratio differences/standard error of the difference.

Habitat	BB	BLCrop	Cereal	CSA	GRSA	KSA	Othcropsa	Other	Other-veg	Rank
BB	-	+8.153 ***	+5.572 ***	+5.016 ***	+8.855 ***	+7.903 ***	+6.656 ***	+13.529 ***	+9.234 ***	1
BLCrop	-8.153 ***	-	-3.588 ***	-4.520 ***	-2.917 **	-2.290 *	-3.325 **	+3.533 ***	-2.767 **	8
Cereal	-5.572 ***	+3.588 ***	-	-0.605 ns	+1.973 ns	+2.533 *	+0.706 ns	+10.051 ***	+3.265 **	3
CSA	-5.016 ***	+4.520 ***	+0.605 ns	-	+2.563 *	+2.081 *	+1.327 ns	+12.552 ***	+3.214 **	2
GRSA	-8.855 ***	+2.917 **	-1.973 ns	-2.563 *	-	+0.385 ns	-1.213 ns	+9.590 ***	+0.843 ns	5
KSA	-7.903 ***	+2.290 *	-2.533 *	-2.081 *	-0.385 ns	-	-1.148 ns	+7.470 ***	+0.176 ns	6
Othcropsa	-6.656 ***	+3.325 **	-0.706 ns	-1.327 ns	+1.213 ns	+1.148 ns	-	+7.494 ***	+1.688 ns	4
Other	-13.529 ***	-3.533 ***	-10.051 ***	-12.552 ***	-9.590 ***	-7.470 ***	-7.494 ***	-	-18.714 ***	9
Other_veg	-9.234 ***	+2.767 **	-3.265 **	-3.214 **	-0.843 ns	-0.176 ns	-1.688 ns	+18.714 ***	-	7

Appendix 3, Table b: Log ratio difference matrix for investigating breeding *yellowhammer* habitat use within 191m of all nests found relative to habitat availability. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability than would be expected. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	BB	BLCrop	Cereal	CSA	GRSA	KSA	Othcropsa	Other	Other-veg	Rank
BB	-	+0.906 ns	-0.373 ns	+1.259 ns	+3.089 **	+0.659 ns	+2.155 *	+4.185 ***	-0.297 ns	3
BLCrop	-0.906 ns	-	-1.048 ns	-0.283 ns	+1.571 ns	-0.437 ns	+0.278 ns	+1.367 ns	-1.121 ns	6
Cereal	+0.373 ns	+1.048 ns	-	+1.684 ns	+3.271 ***	+0.968 ns	+2.630 ns	+6.815 ***	+0.174 ns	1
CSA	-1.259 ns	+0.283 ns	-1.684 ns	-	+2.355 ns	-0.269 ns	+1.073 ns	+15.189 ***	-1.559 ns	5
GRSA	-3.089 **	-1.571 ns	-3.271 ***	-2.355 ns	-	-3.060 **	-1.936 ns	-0.554 ns	-3.247 **	9
KSA	-0.659 ns	+0.437 ns	-0.968 ns	+0.269 ns	+3.060 **	-	+0.982 ns	+2.950 **	-0.954 ns	4
Othcropsa	-2.155 *	-0.278 ns	-2.630 ns	-1.073 ns	+1.936 ns	-0.982 ns	-	+1.484 ns	-2.487 *	7
Other	-4.185 ***	-1.367 ns	-6.815 ***	-15.189 ***	+0.554 ns	-2.950 **	-1.484 ns	-	-8.378 ***	8
Other_veg	+0.297 ns	+1.121 ns	-0.174 ns	+1.559 ns	+3.247 **	+0.954 ns	+2.487 *	+8.378 ***	-	2

Appendix 3, Table c: Log ratio difference matrix for examining *skylark* habitat use, 2000-2002 whilst *provisioning* chicks, with availability in the foraging range (radius 118m around the nest). Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	BB	BLCrop	Cereal	GRSA	Mansa	Other	Other-veg	Rank
BB	-	+0.208 ns	+0.369 ns	-0.752 ns	-5.04 ***	+2.408 *	+2.705 **	3
BLCrop	-0.208 ns	-	-0.873 ns	-1.436 ns	-3.519 **	+1.475 ns	+2.286 *	4
Cereal	-0.369 ns	+0.873 ns	-	+0.001 ns	-3.821 ***	+4.998 ***	+2.436 *	3
GRSA	+0.752 ns	+1.436 ns	-0.001 ns	-	-3.384 **	+2.765 **	+4.212 ***	3
Mansa	+5.04 ***	+3.519 **	+3.821 ***	+3.384 **	-	+6.587 ***	+11.753 ***	1
Other	-2.408 *	-4.998 ***	-4.998 ***	-2.765 **	-6.587 ***	-	-0.658 ns	6
Other_veg	-2.705 **	-2.436 *	-2.436 *	-4.212 ***	-11.753 ***	+0.658 ns	-	5

Appendix 3, Table d: Log ratio difference matrix for examining *sky/ark* habitat use for nesting, 2000-2002, within a radius of 118m around nests involved in foraging watches relative to habitat availability across the study site. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	BB	BLCrop	Cereal	CSA	GRSA	KSA	Othercropsa	Other	Other-veg	Rank
BB	-	+5.936 ***	+4.922 ***	+2.986 **	+5.894 ***	+7.945 ***	+4.340 ***	+9.693 ***	+7.301 ***	1
BLCrop	-5.936 ***	-	-1.694 ns	-3.487 ***	-2.321 *	-0.835 ns	-2.426 *	+2.628 *	-1.441 ns	8
Cereal	-4.922 ***	+1.694 ns	-	-1.792 ns	+0.050 ns	+1.789 *	-0.497 ns	+5.565 ***	+1.317 ns	4
CSA	-2.986 **	+3.487 ***	+1.792 ns	-	+1.769 *	+2.638 *	+1.052 ns	+8.293 ***	+3.132 **	2
GRSA	-5.894 ***	+2.321 *	-0.05 ns	-1.769 *	-	+2.000 ns	-10.728 ***	+8.778 ***	+2.145 *	5
KSA	-7.903 ***	+0.835 ns	-1.789 *	-2.638 *	-2.000 ns	-	-1.886 ns	+4.622 ***	-0.728 ns	7
Othercropsa	-4.340 ***	+2.426 *	+0.497 ns	-1.052 ns	+10.728 ***	+1.886 ns	-	+5.760 ***	+1.851 ns	3
Other	-9.693 ***	-2.628 *	-5.565 ***	-8.293 ***	-8.778 ***	-4.622 ***	-5.760 ***	-	-12.334 ***	9
Other_veg	-7.301 ***	+1.441 ns	-1.317 ns	-3.132 **	-2.145 *	+0.728 ns	-1.851 ns	+12.334 ***	-	6

Appendix 3, Table e: Log ratio difference matrix for examining *yellowhammer* habitat use whilst *provisioning* chicks, with availability in the foraging range. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability than would be expected. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	BB+GRSA	BLCrop	Cereal	CropSA	KSA	Other	Other-veg	Rank
BB+GRSA	-	+0.302 ns	-1.090 ns	+0.693 ns	+0.090 ns	+2.582 *	+2.588 *	2
BLCrop	-0.302 ns	-	-1.125 ns	-0.919 ns	+1.140 ns	+2.290 *	+1.920 ns	4
Cereal	+1.090 ns	+1.125 ns	-	+0.541 ns	+2.533 *	+5.499 ***	+5.310 ***	1
CropSA	-0.693 ns	+0.919 ns	-0.541 ns	-	+1.075 ns	+2.737 *	+2.057 ns	3
KSA	-0.090 ns	-1.140 ns	-2.533 *	-1.075 ns	-	+1.824 ns	+2.007 ns	5
Other	-2.582 *	-2.290 *	-5.499 ***	-2.737 *	-1.824 ns	-	-0.759 ns	7
Other_veg	-2.588 *	-1.920 ns	-5.310 ***	-2.057 ns	-2.007 ns	+0.759 ns	-	6

Appendix 3, Table f: Log ratio difference matrix for examining provisioning *yellowhammer* habitat use within 191m of each nest involved in a foraging watch relative to habitat availability across the study site. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability than would be expected. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	BB	BLCrop	Cereal	CSA	GRSA	KSA	Othcropsa	Other	Other-veg	Rank
BB	-	+1.346 ns	+0.119 ns	+1.454 ns	+2.040 ns	+1.130 ns	+0.285 ns	+3.438 **	+0.406 ns	1
BLCrop	-1.346 ns	-	-1.237 ns	-0.773 ns	-0.074 ns	-0.493 ns	-1.118 ns	+0.553 ns	-1.184 ns	8
Cereal	-0.119 ns	+1.237 ns	-	+1.438 ns	+2.245 *	+1.339 ns	+0.227 ns	+8.686 ***	+0.865 ns	2
CSA	-1.454 ns	+0.773 ns	-1.438 ns	-	+0.121 s	+0.129 ns	-1.438 ns	+10.679 ***	-1.096 ns	5
GRSA	-2.040 ns	+0.074 ns	-2.245 *	-0.121 ns	-	-0.945 ns	-2.242 *	+1.067 ns	-2.209 *	7
KSA	-1.130 ns	+0.493 ns	-1.339 ns	-0.129 ns	+0.945 ns	-	-0.824 ns	+2.034 ns	-1.100 ns	6
Othcropsa	-0.285 ns	+1.118 ns	-0.227 ns	+1.438 ns	+2.242 *	+0.824 ns	-	+2.885 *	+0.050 ns	3
Other	-3.438 **	-0.553 ns	-0.865 ns	-10.679 ***	-1.067 ns	-2.034 ns	-2.885 *	-	-7.870 ***	9
Other_veg	-0.406 ns	+1.184 ns	-1.206 ns	+1.096 ns	+2.209 *	+1.100 ns	-0.050 ns	+7.870 ***	-	4

Appendix 3, Table g: Log ratio difference matrix for comparing provisioning *yellowhammer* and *skylark* habitat use relative to habitat availability across the study site in 2000. Ns – not significant. The highest rank indicates the greatest difference in habitat use between the two species and the lowest rank indicates the least difference in habitat use. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	BB+GRSA	BLCrop	Cereal	Cropsa	KSA	Other	Other-veg	Rank
BB+GRSA	-	-0.583 ns	+ 0.703 ns	-0.930 ns	+0.636 ns	-1.234 ns	-0.298 ns	6
BLCrop	+0.583 ns	-	-0.589 ns	+0.694 ns	-0.862 ns	+0.689 ns	-1.323 ns	4
Cereal	-0.703 ns	+0.589 ns	-	+0.212 ns	+1.440 ns	-0.068 ns	+1.084 ns	2
Cropsa	+0.930 ns	-0.694 ns	-0.212 ns	-	-0.769 ns	+0.127 ns	-0.926 ns	6
KSA	-0.636 ns	+0.862 ns	-1.440 ns	+0.769 ns	-	+0.115 ns	+0.997 ns	2
Other	+1.234 ns	-0.689 ns	+0.068 ns	-0.127 ns	-0.115 ns	-	-0.955 ns	6
Other_veg	+0.298 ns	+1.323 ns	-1.084 ns	+0.926 ns	-0.997 ns	+0.955 ns	-	2

Appendix 3, Table h: Log ratio difference matrix for examining *song thrush* habitat use 2000-2002 whilst *provisioning* chicks within the minimum convex polygon foraging area around the nest ($n = 22$). Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	Allsa	Bound	Cereal	Grass_veg	Herb_veg	Other	PP	Wood	Rank
Allsa	-	-1.450 ns	+0.409 ns	-1.553 ns	-0.359 ns	-1.252 ns	+0.323 ns	-2.889 **	6.5
Bound	+1.450 ns	-	+1.701 ns	+2.467 *	+0.475 ns	-0.780 ns	+1.003 ns	-0.912 ns	3
Cereal	-0.409 ns	-1.701 ns	-	-0.918 ns	-0.810 ns	-1.895 ns	-0.152 ns	-2.317 *	8
Grass_veg	+1.553 ns	-2.467 *	+0.918 ns	-	+0.772 ns	-2.969 **	-0.907 ns	-1.238 ns	4.5
Herb_veg	+0.359 ns	-0.475 ns	+0.810 ns	-0.772 ns	-	-1.224 ns	+0.265 ns	-1.751 ns	4.5
Other	+1.252 ns	+0.781 ns	+1.895 ns	+2.969 **	+1.224 ns	-	+0.991 ns	-0.431 ns	2
PP	-0.323 ns	-1.003 ns	+0.152 ns	+0.907 ns	-0.265 ns	-0.991 ns	-	-1.513 ns	6.5
Wood	+2.889 **	+0.912 ns	+2.317 *	+1.238 ns	+1.751 ns	+0.431 ns	+1.513 ns	-	1

Appendix 3, Table i: Log ratio difference matrix for examining *song thrush* habitat use 2000-2002 (whilst *provisioning* chicks) of the minimum convex polygon foraging area around the nest (n = 22) with the availability of habitats across the study site. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	Allsa	BLCrop	Bound	Cereal	Garden	Grass_veg	Herb_veg	Other	PP	Wood	Rank
Allsa	-	+1.087 ns	-3.385 **	+2.677 *	-1.832 ns	-3.652 **	-3.170 **	-5.142 ***	+0.122 ns	-5.446 ***	7
BLCrop	-1.087 ns	-	-3.792 ***	+1.351 ns	-1.935 ns	-2.847 **	-3.082 **	-3.994 ***	-0.771 ns	-4.412 ***	9
Bound	+3.385 **	+3.792 ***	-	+6.930 ***	+2.126 *	+1.848 ns	-0.113 ns	-1.557 ns	+2.990 **	-1.719 ns	4
Cereal	-2.677 *	-1.351 ns	-6.930 ***	-	-3.584 **	-6.113 ***	-5.129 ***	-4.091 ***	-2.254 *	-7.670 ***	10
Garden	+1.832 ns	+1.935 ns	-2.126 *	+3.584 **	-	-0.664 ns	-1.561 ns	-3.691 **	+1.548 ns	-3.127 **	6
Grass_veg	+3.652 **	+2.847 **	-1.848 ns	+6.113 **	+0.664 ns	-	-1.153 ns	-3.767 **	+2.458 *	-5.606 ***	5
Herb_veg	+3.170 **	+3.082 **	+0.113 ns	+5.129 ***	+1.561 ns	+1.153 ns	-	-0.957 ns	+2.55 *	-1.564 ns	3
Other	+5.142 ***	+3.994 ***	+1.557 ns	+4.091 ***	+3.691 **	+3.767 **	+0.957 ns	-	+3.894 ***	-1.172 ns	2
PP	-0.122 ns	+0.771 ns	-2.990 **	+2.254 *	-1.548 ns	-2.458 *	-2.55 *	-3.894 ***	-	-4.062 ***	8
Wood	+5.446 ***	+4.412 ***	+1.719 ns	+7.670 ***	+3.127 **	+5.606 ***	+1.564 ns	+1.172 ns	+4.062 ***	-	1

Appendix 3, Table j: Log ratio difference matrix for examining *song thrush* habitat use post-fledging chicks 2000-2002 with availability in the study area. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the habitat used most relative to its availability and the lowest rank indicates the habitat used least relative to its availability. A positive log ratio difference indicates the row habitat was used more than the column habitat relative to their availability.

Habitat	Allsa	BLCrop	Bound	Cereal	Garden	Grass veg	Herb veg	Other	PP	Wood	Rank
Allsa	-	+1.684 ns	-3.002 **	+1.219 ns	-1.406 ns	-3.656 **	-6.882 ***	-6.478 ***	-0.194 ns	-8.074 ***	8
BLCrop	-1.684 ns	-	-3.857 **	-0.226 ns	-1.995 ns	-3.136 **	-4.684 ***	-4.550 ***	-1.133 ns	-5.847 ***	10
Bound	+3.002 **	+3.857 **	-	+4.112 **	+1.737 ns	+1.758 ns	-1.365 ns	-2.178 *	+2.091 ns	-2.630 *	4
Cereal	-1.219 ns	+0.226 ns	-4.112 **	-	-1.907 ns	-3.229 **	-4.395 ***	-3.483 **	-1.008 ns	-5.692 ***	9
Garden	+1.406 ns	+1.995 ns	-1.737 ns	+1.907 ns	-	-0.185 ns	-2.810 *	-4.458 ***	+1.01 ns	-3.729 **	6
Grass_veg	+3.656 **	+3.136 **	-1.758 ns	+3.229 **	+0.185 ns	-	-4.514 ***	-5.828 ***	+1.455 ns	-9.823 ***	5
Herb_veg	+6.882 ***	+4.684 ***	+1.365 ns	+4.395 ***	+2.810 *	+4.514 ***	-	+0.270 ns	+4.97 ***	-2.140 ns	2
Other	+6.478 ***	+4.550 ***	+2.178 *	+3.483 ***	+4.458 ***	+5.828 ***	-0.270 ns	-	+4.138 **	-2.218 *	3
PP	+0.194 ns	+1.133 ns	-2.091 ns	+1.008 ns	-1.01 ns	-1.455 ns	-4.97 ***	-4.138 **	-	-4.802 ***	7
Wood	+8.074 ***	+5.847 ***	+2.630 *	+5.692 ***	+3.729 **	+9.823 ***	+2.140 ns	+2.218 *	+4.802 ***	-	1

CHAPTER 4

RELATIVE INFLUENCE OF VEGETATION STRUCTURE AND INVERTEBRATE ABUNDANCE ON PROVISIONING BIRDS

4.1 Summary

1. There is circumstantial and direct evidence to suggest that vegetation structure has a greater influence on habitat use by provisioning birds than invertebrate abundance (Odderskaer et al., 1997; Chamberlain et al., 1999a; Morris et al., 2001b). This chapter aims to evaluate and compare the microhabitat of foraging and control sites of provisioning birds within the same habitat type. This was examined by investigating vegetation structure (height and density), botanical species composition (number of species and percentage cover of grouped species) and invertebrate abundance.
2. There were no significant differences between the vertical vegetation density of skylark foraging and control sites, although there appeared to be a trend for less dense vegetation structure in foraging sites in all habitat types examined. Skylarks foraged in areas with significantly more bare ground and less crop cover in winter cereals and less crop cover in beans, when compared to control areas (i.e. percentage ground cover). No significant difference was detected in botanical species richness at either of these sites, although in 2002 there were significantly more species present in cropped habitats compared to 2001 but fewer in set-aside. There was no evidence to suggest that skylarks selected areas of higher invertebrate abundance for foraging.
3. The unique opportunity was taken to compare skylark and yellowhammer foraging sites using data collected in 2000. Skylarks foraged in areas with significantly less broadleaved crop than yellowhammers did in set-aside, and also in areas with significantly more araneae in winter wheat than did yellowhammers. There were no differences in botanical species richness or in vertical height structure at foraging sites of the two species.
4. For the song thrush, no difference was found between the vertical vegetation structure between foraging and control sites within the foraging range, or between the foraging and home range. Differences in woodland vegetation structure were detected between months, with June having significantly denser vegetation than July, but there was no difference in vegetation structure between height categories. No significant differences in invertebrate abundance were detected between song thrush foraging and control sites in the foraging range although there appeared to be more invertebrates present in foraging than control sites in grass, woodland and boundary habitats. There

was significantly greater worm biomass in boundary habitats of birds foraging for themselves rather than for nestlings.

5. The sampling techniques used to explore why provisioning birds foraged at selected sites within different habitat types may have been too conservative to reveal any differences between them. As a result, there is little evidence to support the hypothesis that vegetation structure had a greater influence on provisioning birds than invertebrate abundance, or to suggest that invertebrate abundance determines habitat use by provisioning birds, independently of habitat structure. Nonetheless, vegetation structure is likely to determine where skylarks forage. In the case of the song thrush, invertebrate abundance is more likely to determine foraging habitat use. Other factors that were not examined here, such as predation pressure, soil moisture and penetrability are also likely to influence where birds forage.
6. Results suggest that cereal crop management that encourages a less dense crop structure with patches of bare ground could assist provisioning skylarks and possibly yellowhammers.

4.2 Introduction

The relative influence of vegetation structure and invertebrate abundance on provisioning birds is little studied or understood. Although several studies have discussed the significance that food availability and/or its accessibility may have on habitat use by provisioning birds (Odderskaer et al., 1997; Wilson et al., 1997a; Vickery & Fuller, 1998; Chamberlain et al., 1999a; Wilson, 2001; Morris et al., 2001b; Perkins et al., 2002) there is only one published study that attempts to measure their joint effects on a farmland bird species within the UK; the yellowhammer (Morris et al., 2001b). It was found that yellowhammers foraged in areas of sparser vegetation with more invertebrates, within winter cereals, than in areas sampled randomly. This would suggest that vegetation structure is as important as invertebrate abundance to foraging birds. In contrast, a study by Odderskaer et al. (1997), in Denmark, suggested that skylarks compromised where they foraged in winter cereals by selecting areas with lower invertebrate abundance that allowed ease of movement, in this instance foraging in tramlines and unsown plots rather than within the crop itself despite invertebrate abundance being higher there.

Although farmland offers a wide range of diverse cropped and uncropped habitat types to many bird species, and hence a wide range of vegetation structures in which to forage, agricultural intensification since the Second World War has greatly changed the structure and diversity of these habitats through management (for examples see Stoate, 1996; Pain & Pienkowski, 1997; Fuller, 2000). In addition, cultivations and applications of agrochemicals applied over a crop year, (pesticides, herbicides and insecticides), are known to affect numbers and distribution of invertebrate species and their host plant vegetation structure and abundance (Edwards, 1977, 1984; Luff, 1987; Campbell et al., 1997; Wilson et al., 1997b; Ewald & Aebischer, 1999). Invertebrate diversity and abundance varies between habitats. For example, cereals hold lower densities of sawfly and lepidoptera larvae and earthworms than natural grassland, set-aside and other less intensively managed habitats (Edwards, 1977; Edwards & Loft, 1982; Booij & Noorlander, 1992; Moreby & Aebischer, 1992; Peach et al., 2004). Furthermore, invertebrate abundance declines with distance into the crop, with field margins, crop edges and hedges having greater invertebrate abundances (Thomas et al., 1991; Moreby & Aebischer, 1992; Thomas & Marshall, 1999).

Farmland skylarks, which nest solely on the ground in fields, require territories that encompass large open areas. These areas are most commonly cropped habitats due to the recent loss of habitat diversity with agricultural intensification. However, territory densities are known to decrease as crop height increases during the breeding season (Schl pfer, 1988; Toepfer & Stubbe, 2001) and potentially fewer nesting attempts per pair can be made within this habitat type (Schl pfer, 1988; Wilson et al., 1997a; Chamberlain & Crick, 1999; Chamberlain et al., 1999a; Donald et al., 2001b), thereby contributing to the national decline of the population. The developing crop sward structure of winter cereals may reduce territory density (e.g. Chamberlain et al., 1999a) by affecting (i) the suitability of the cropped habitat for nesting (Jenny, 1990a; Donald & Vickery, 2000; Donald et al., 2001b) and (ii) accessibility for foraging (Odderskaer et al., 1997; Wilson, 2001; Morris et al., 2001a; Morris et al., 2001b), which could force birds to nest and forage in sub-optimal areas. Yellowhammers are also associated with cereal crops on arable farmland, being largely granivorous although nestling diet comprises mainly invertebrates (Stoate et al., 1998). Foraging vegetation structure and invertebrate abundance are therefore likely to affect this species in similar ways to the skylark.

There is a limited amount of literature available on the effects of vegetation structure on provisioning farmland song thrushes, which forage mainly in woodland, grassland, wet ditches and gardens (Peach et al., 2002; Peach et al., 2004) and are therefore less likely to be affected by sward structure in cereals. Earthworms are most abundant in damp, undisturbed fields, rich in organic matter (Edwards & Lofty, 1977). Peach et al. (2004) found earthworm biomass was greater in woodland and grassland, possibly because these habitats dried out more slowly in comparison to others such as cereal fields. However, this could also be due to the lack of mechanical damage and the potentially increased food availability (Edwards & Lofty, 1982; Edwards, 1984; Tucker, 1992; Edwards & Bohlen, 1996). On grassland, increased stocking densities and earlier, more frequent, mowing of grass crops as silage for winter fodder can affect vegetation structure and reduce surface invertebrate abundance. For the benefit of skylarks, Wakeham-Dawson et al. (1998a) proposed a combination of sward heights (15 - 25cm) on arable reversion grassland, providing taller areas for both nesting and feeding, since heavy grazing may produce unsuitable nesting habitat and have a detrimental effect on food abundance and territory numbers. In contrast, for song thrush, grazed pasture holds a relatively rich source of earthworms (Tucker, 1992), readily accessible to invertebrate feeding birds (Wilson et al., 1996). Observations of foraging song thrushes suggest that short grass makes earthworm accessibility easier than long and unmanaged grass.

Few studies have examined the effects of vegetation structure, botanical species composition and invertebrate abundance at selected foraging sites of ground-feeding farmland bird species (Morris et al., 2001b). The review by Aebischer et al. (2000) has shown that different declining bird species requirements, in terms of physical vegetation structure and invertebrate prey, can be met through set-aside and agri-environment schemes but a greater understanding of individual species' needs is essential if more declines are to be reversed. As seen in Chapter 3, skylark, yellowhammer and song thrush did not forage randomly across the available farmland. This chapter therefore aims to i) assess and compare the microhabitat of areas where birds chose to forage with those where they did not so and ii) to try to establish what factors at foraging sites were influencing provisioning adults by investigating vegetation structure, botanical species and the invertebrate abundance at these sites.

4.3 Methodology

4.3.1 Skylark and yellowhammer

4.3.1.1 *Vegetation surveying of foraging places*

Immediately following each foraging watch (described in Chapter 3) sites where adult birds were observed foraging were marked using fibreglass canes. If a bird was seen foraging within the same habitat type (Table 1) within 10m of a previous sortie this was taken to be the same foraging area, although each individual sortie was recorded on the map surrounding the nest site area to allow distance travelled to be measured. In 2000 and 2001, 1 - 6 vegetation samples were taken from each foraging habitat during a single watch, depending on the number of habitats used (see 4.3.1.2 and 4.3.1.3). However in 2002, due to time constraints, a maximum of 3 foraging and 3 control vegetation site samples were collected from each habitat type. For the purposes of this data analysis all vegetation samples taken from set-aside were grouped together, regardless of where they were taken, e.g. beetle banks, first year or second year kale etc.

For each foraging place the following data were collected.

4.3.1.2 *Vegetation cover density*

Vertical vegetation density was measured as the percentage of a graduated 1m -'cover density' board that was covered at each of 11 height categories (H1 – H11) from a distance of two metres away, (0-5cm, 5-10cm, 10-20cm, 20-30cm, 30-40cm, 40-50cm, 50-60cm, 60-70cm, 70-80cm, 80-90cm, 90-100cm) (Chapter 2, Appendix 2, Plate 1). This was repeated at each site four times, moving the board 90° each time. A replicate was taken at the second quadrat sampling point, i.e. two sub-samples (see 4.3.1.3).

4.3.1.3 Plant cover estimates and species richness at foraging sites

Different plant species percentage cover and percentage bare ground was estimated by eye within each foraging area using a 0.25m² quadrat placed on the ground. The number of plant species present was also recorded. A replicate was taken around 3m from the first sampling point.

Table 1: 'Available' foraging habitats used by skylark, song thrush and yellowhammer in the vegetation analysis.

Bird species	Available foraging habitat type	Available 'vegetation' type within each habitat
<i>Skylark and yellowhammer</i>	Winter wheat	Cereal crop, perennial and annual grasses and dicotyledons, bare ground.
	Winter barley	Cereal crop, perennial and annual grasses and dicotyledons, bare ground.
	Track	Farm tracks, perennial and annual grasses and dicotyledons, bare ground.
	Set-aside	All types, including grass tracks (see Table 1, Chapter 3), perennial and annual grasses and dicotyledons, bare ground.
	Oilseed rape	Broadleaved crop, perennial and annual grasses and dicotyledons, bare ground.
<i>Song thrush</i>	Woodland	Old and new woodland
	Grass habitats	Permanent pasture, grass track, garden
	Boundary	Field margin, verge, hedge and ditch, rough grass strips, short herbaceous vegetation
	Tall herbaceous	Embankment, tall herbaceous vegetation.
	Cereal and Broadleaved crops	Winter wheat, winter barley, beans and oilseed rape

4.3.1.4 Invertebrate abundance

Ground dwelling invertebrates were sampled using a Dietrick-Vacuum (D-vacuum) suction sampler at the marked foraging areas in order to assess food availability and abundance to provisioning adults (Chapter 4,

Appendix 4, Plate 1). Two 0.5m² D-vacuum samples were taken, each comprising five sub-samples of 0.1m² 10-second durations over an approximate area of 2 - 3m² during dry weather only. This sampling strategy was considered to be the most suitable for sampling insects available to foraging birds at the time of the foraging watch, although it may not be the most appropriate for sampling larger insects such as carabids or caterpillar and sawfly larvae (Mommertz et al., 1996; Collins, 1999), which are important constituents of both skylark and yellowhammer chick diet. This sampling strategy also assumed that samples were representative of invertebrates available to birds at their foraging sites. The samples were transferred to plastic bags and frozen before being stored in 80% alcohol ready for identification. In 2000, D-vacuum samples were taken after each foraging watch, but in 2001 and 2002 from the first watch only. For 2000, samples from June and July only were identified to family or order level under a binocular microscope, enabling a comparison of skylark and yellowhammer foraging sites to be made during the main breeding period. Time constraints limited which of the numerous samples taken that season could be analysed. For 2001 and 2002, all invertebrate samples were identified.

4.3.1.5 Control data

In order to investigate whether birds foraged at random within the vegetation structure of different habitat types in the foraging range, control samples of vegetation cover density, species composition and richness, and invertebrate abundance were taken. Control samples were taken at least 50m away from the nearest foraging point within the same habitat type, and if they were to be taken in a crop, at least 12m from the crop edge, to alleviate crop edge differences in invertebrate abundance (Moreby & Aebischer, 1992). Again two sub-samples of each type of data collected were taken, using the same methodology as above. For skylarks, control samples were taken in 2001 and 2002 only. No control samples were taken for yellowhammers.

4.3.2 Song thrushes

In order to examine the vegetation structure and invertebrate abundance at song thrush foraging sites the minimum convex polygon (MCP), plotted by hand immediately after the foraging data were collected (see Chapter 3 section 3.3.3.2), was used. On average vegetation and invertebrate samples were collected within 1

- 2 days of this. This allowed estimation of the vegetation structure within song thrush foraging habitats at the time of provisioning nestlings, and generally whilst chicks were still in the nest.

Within the hand-drawn MCP each fix, using the centre of the triangle, was plotted to the nearest intersection onto a habitat map covered by a 10 x 10m grid. This MCP was considered to be a rough outline of the area where each bird was likely to be foraging at the time fixes were taken. Due to the inherent errors associated with this technique (see Chapter 3), a protocol was developed to standardise the location of points for the collection of 'foraging data'. First, the number of different foraging habitat types within each MCP was listed using the plotted fix points. From those habitats, sampling positions were identified using the step-wise procedure below. Figure 1 accompanies the below text, helping illustrate the procedure for determining foraging and control sampling points from fix points within the song thrush MCP.

Foraging samples from each habitat type;

1. A foraging sample point was selected according to the maximum density of fix points around 9 loci on the grid covering the mapped MCP. The central locus was an ideal foraging sample point.
2. Foraging samples were taken at least 10m apart.
3. Foraging samples were not to be taken on the MCP boundary unless they could not be placed anywhere else. If foraging samples could not be placed within the MCP a 10m boundary around the MCP was marked out if necessary, 'loosening' the MCP boundary.
4. Foraging samples were not taken on a habitat edge. If a fix point occurred on a habitat edge it was treated as two separate points – one for each habitat type.
5. If the habitat type contained two discrete elements (e.g. ditch and hedge) one sample was taken from each habitat.
6. If fixes fell on an unrealistic habitat type, e.g. pond, building or road, the fix was relocated accordingly: the next nearest habitat was determined, the fix was placed in the mid-point of the two appropriate loci of the habitat.

Control samples from each habitat type;

1. A control sample point was selected according to areas with the minimum number of fixes (ideally none) and that were greater than 10m from a used 'foraging sample' locus.
2. Control samples were not taken on the MCP boundary. If control samples could not be placed within the MCP a 10m boundary around the MCP was marked out if necessary, 'loosening' the MCP boundary.
3. Control samples were not taken at the habitat edge.
4. If there was a distance of less than 10m between the foraging and control sample site points in small areas, e.g. hedge/ditch complex this was accepted if there was no alternative sampling place.
5. Ideally control samples were taken as close to the nest site as possible since birds were actively flying over the area to forage elsewhere.

A hand-held GPS was used to find the selected grid locations and fibreglass canes were used to mark them. Soil cores, measuring 10 x 10 x 10cm, were taken early in the morning from both the control and foraging sites. Following this, cover density was recorded at both control and foraging sites (using methods in section 4.3.1.2). Soil samples were sorted by hand the same day, carefully teasing apart the soil with forceps. All invertebrates were washed in alcohol to remove excess soil and to kill them, blotted dry and weighed to the nearest 0.1g. The number of worms per core, group worm weight per core and any slugs, snails and miscellaneous invertebrates (such as tipulidae larvae, woodlouse, coleoptera, millipedes and other larvae) were recorded and included in the total invertebrate weight. Soil type, field location and date were recorded.

The number of control and foraging samples taken varied between years:

2000 - five soil cores and cover density boards from foraging habitats only (during the pilot study to see what was feasible, but not used in the analysis).

2001 - no control samples were taken after mid – June (due to unforeseen logistical problems). When controls were taken, 2 soil cores and 2 cover density board measurements were taken at two foraging sites (one at each site) and two controls to these sites. When no controls were taken 3 soil cores and 3 cover density board measurements were taken from within each habitat type.

2002 - Control and foraging samples were taken for each tagged bird. 5 soil cores and 3 cover density board samples were collected per habitat type.

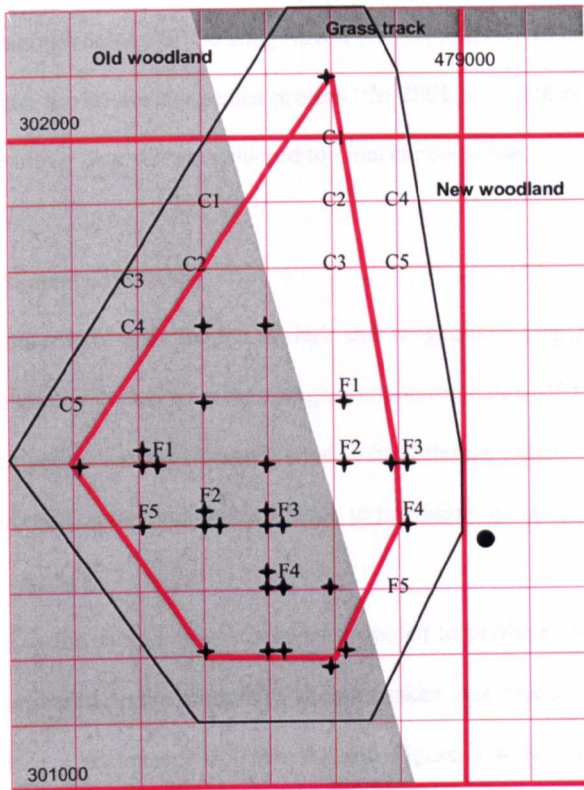


Figure 1: An illustration to accompany the text of 4.3.2 showing where 5 song thrush foraging and control sample points were selected within the Minimum Convex Polygon (MCP) in old (grey) and new woodland (white) habitats from fixes plotted on a 10m x 10m British National grid. The MCP is encompassed within the red border and the 'loosened' MCP is contained within the black border. The black circle is the nest and the stars are fix points. C1-C5 and F1-F5 within each habitat would be taken on the grid intersections. 30 fixes were plotted to make the MCP, size 0.27ha with a range width of 91m.

4.4 Data analysis

For skylark and yellowhammer, at each observed foraging site vegetation cover density (vertical structure), botanical species composition, number of plant species was recorded and d-vacuum samples taken. The same

data were collected for control samples for skylarks in 2001 and 2002. For song thrush, only vegetation cover density and soil core samples were taken at each foraging and control site in order for a comparison to be made between them. Due to constraints on time, plant species composition was not investigated since it was assumed that the foraging ecology of the song thrush was more likely to be influenced by vegetation structure and density rather than the botanical species present. In 2001, soil probes to measure soil penetrability were also taken but the resulting data were considered too inaccurate to use.

These details were compared between:

1. Foraging and control sites for the skylark and song thrush (separately) for 2001 and 2002. For the song thrush data collected from the foraging and home range MCP was used.
2. Skylark and yellowhammer foraging sites in six different habitat categories in order to try to identify factors important, at the microhabitat level, to provisioning adults.

The 'nest' was used as the sample unit. Data were pooled to produce mean values per nest per habitat type and a weight function based on the number of samples taken was used in all analyses. Weighted transformed means are expressed \pm 1SE (except in Table 11 and Figure 6 where back-transformed data are presented). Analyses were conducted using Genstat vs 6 and Systat vs 10.

4.4.1 Vegetation structure at foraging sites

Percentage vegetation cover density from each foraging location was averaged and normalized using an arcsine square root transformation at each of the eleven height categories. To avoid pseudo-replication, cover density board measurements were averaged at each height category.

4.4.1.1 Comparison between skylark foraging and control sites:

The paired difference between foraging and control sites was calculated for all data (and used as the dependent data). A nested multivariate analysis of variance (MANOVA) was used to test whether nest (factor) had a significant effect, using nest (factor) nested within year and carrying out analysis on the cover densities across

all height categories, within winter wheat, winter barley, beans, set-aside, and track. Since nest was significant for all habitat types, except beans, the means of the paired differences per nest were calculated. Height categories were pooled into 5 new categories (H1-3 – 0-20cm, H4-5 – 20-40cm, H6-7 – 40-60cm, H8-9 – 60-80cm and H10-11 – 80-100cm), since there was insufficient replication (number of nests) for the number of height categories in the original analysis. A multivariate repeated measures analysis was used with height category as the repeated measures factor to determine the effect of year, height, and year*height interactions. A weighting variable was added, determined by the number of cover density boards taken. No statistical comparison was made between foraging and control vegetation structure differences in oilseed rape because only one skylark pair was observed foraging in it ($n = 1$) or winter oats since it was used only in 2002 ($n = 3$).

4.4.1.2 Comparison between skylark and yellowhammer foraging sites:

All data relating to a single nest were then pooled to produce a single mean percentage cover value for each of the eleven height categories. Separate comparisons of vegetation structure of skylark and yellowhammer foraging sites were made in winter wheat, winter oilseed rape, track, set-aside and winter beans, using MANOVA, with the eleven height categories as the dependent variables and bird species as the independent variable. A weighting variable was added, using the number of cover density boards taken in each habitat type. When comparing between skylark and yellowhammer foraging structure differences, winter barley was excluded from the analysis since only yellowhammers used it to forage in.

4.4.1.3 Comparison between song thrush foraging and control sites within the foraging range:

The same analytical procedure as described in sub-section 4.4.1.1 was used to compare data within 4 foraging habitat types; woodland, boundary + tall herbaceous vegetation, grass habitats (permanent pasture + grass track + garden) and boundary alone. Habitats categories 'boundary and tall herbaceous vegetation' and 'permanent pasture, grass track and garden' were combined because their relative structure was similar and very few samples (i.e. nests) were taken from grass track ($n = 1$), garden ($n = 1$) and tall herbaceous vegetation ($n = 3$). No comparisons were made between cereal ($n = 2$) and broadleaved crops ($n = 4$) due to the small number of samples taken there in each year.

4.4.1.4 Comparison between song thrush foraging sites within the foraging and home range:

No control sample data were taken for several nests within the foraging and home range after mid-June in 2001, due to constraints in time. Sample data were collected from within the foraging range and also within home ranges during mid-June, July and August (when birds were not known to have nested) and compared with one another to see whether vegetation height structure differed when birds were provisioning young. Heights were pooled into 5 categories (H1-3 – 0-20cm, H4-5 – 20-40cm, H6-7 – 40-60cm, H8-9 – 60-80cm and H10-11 – 80-100cm), since there were insufficient degrees of freedom (number of nests) to look at each height category separately. A MANOVA was carried out to test for a month effect, using height categories as the dependent variables. Separate comparisons of vegetation structure were made in woodland, boundary+herbaceous vegetation and grass habitats (permanent pasture+grass track+garden). A weighting variable was added, using the number of cover density boards taken in each habitat type for each nest.

4.4.2 Botanical species composition at foraging sites

The different plant species were grouped into eleven categories; winter wheat, winter beans, winter barley, winter oilseed rape, triticale, perennial grasses, annual grasses, annual dicotyledons, perennial dicotyledons, biennial dicots and 'other'. Bare ground was also included in the analysis.

Percentage cover of each category was arcsine square root transformed to normalise the data and then averaged across both quadrats. All data relating to a single nest were pooled to produce a single mean percentage cover value for each of the eleven vegetation categories. Separate comparisons were made between skylark control and foraging points for 2001 and 2002 in each habitat category, in order to determine plant species groups that could influence provisioning birds. Separate comparisons were also made between skylark and yellowhammer foraging sites for five different habitat categories, in order to determine differences in plant species groups in the same habitat types. The number of quadrat samples varied between nests within each habitat type and consequently was used as a weighting variable in the analysis.

Differences in the percentage cover of the eleven plant species categories between skylark foraging and control locations and skylark and yellowhammer foraging locations were analysed separately using ANOVA

to test for year, quadrat type (forage or control) and year*quadrat type effects. Sequential Bonferroni corrections were applied as post hoc tests (Rice, 1988). Bonferroni corrections were used since when multiple comparisons are made on the same data set it is increasingly likely that a significant result should occur, hence accepting a Type 1 error (i.e. the chance that a result is significant when it is not). Bonferroni corrections are a robust method of reducing this error (Rice, 1988).

Habitat categories included winter wheat, winter oilseed rape, set-aside, grass track and beans. During analysis the dependent variable was the vegetation species category and the independent variable was bird species or foraging site (forage or control).

4.4.3 Botanical species richness at foraging sites

The mean number of plant species per quadrat pair was determined in order to test for differences in the number of plant species between i) skylark foraging and control sites and ii) skylark and yellowhammer foraging sites within the same habitat type, using weighted t-tests. The dependent variable was the average number of plant species and the independent variable was bird species or foraging site. Year was tested for separately.

4.4.4 Invertebrate abundance at foraging sites

Invertebrate data were pooled per nest to produce the mean abundance of 12 groupings and transformed with $\log(x+1)$ to normalise the data; Araneae (wolf spiders, non-wolf spiders and opiliones), Other Arthropods (isopoda, chilopoda/diplopoda, also including gastropoda), Other Insects (collembola, neuroptera/mecoptera, orthoptera, dermaptera), Homoptera (delphacidae, cicadellidae, cecropidae), Other Hemiptera (psyllidae, heteroptera, aphidae), Lepidoptera (adults and larvae), Hymenoptera (sawfly adult and larvae), Other Hymenoptera adults (all parasitic wasps and larvae), Coleoptera (carabidae, staphilynidae, and cantharidae (adults and larvae)), Other Coleoptera (coccinellidae, chrysomelidae – adult and larvae, elateridae, nitidulidae, curculionidae, small coleoptera, other coleoptera and other beetle larvae), Diptera (tipulidae, empidae, diptera larvae), Other Diptera (other nematocera, dolichopodidae, statiomyidae, rhagonidae, asilidae, other

brachycera, syrphidae, lonchopteridae, other aschiza, phoridae, opomyza, other acalypts, calypterae, scatophagidae, other diptera) per nest.

4.4.4.1 Comparison between skylark foraging and control sites:

For each invertebrate group, the mean of paired differences between foraging and control sites for each nest in each habitat, was calculated and analysed using a weighted paired t-test first testing for a year effect. If year was not significant a weighted paired t-test was then carried out on the mean abundance of invertebrates between foraging and control sites. Habitat categories included winter wheat, winter barley, set-aside (including grass track) and beans. Bonferroni correction was applied to any significant result because multiple comparisons were being made (Rice, 1988).

4.4.4.2 Comparison between skylark and yellowhammer foraging sites:

Differences between invertebrate group abundance at skylark and yellowhammer foraging sites were determined using weighted t-tests, with sequential Bonferroni corrections. Weighting was determined by the number of times each habitat type was represented per nest. Separate comparisons of invertebrate abundance were made between skylark and yellowhammer foraging sites for winter wheat and set-aside only, due to there being an insufficient comparable number of 'nests' recorded 'foraging' within the other habitat types. Bonferroni correction was applied to any significant result because multiple comparisons were being made (Rice, 1988). Difference in total invertebrate abundance between skylark and yellowhammer foraging sites was also examined.

4.4.4.3 Comparison between song thrush foraging and control sites:

Earthworm biomass was square root transformed to normalise the data. Data were analysed as described in sub-section 4.4.4.1. Habitat categories comprised boundary, woodland, tall herbaceous vegetation, grass habitats and broadleaved crop. There were insufficient data to compare between foraging and control sites in cereals. Bonferroni correction was applied to any significant result since multiple comparisons were being made (Rice, 1988).

4.5 Results

4.5.1 Skylarks

Data from 235 cover density board and botanical species quadrat samples were used in the analysis (146 in 2001 from 15 nests and 89 in 2002, from 7 nests).

4.5.1.1 Vegetation cover density

There were no significant differences in vegetation structure between skylark foraging and control sites. However there is a clear trend towards less dense vegetation at foraging sites than at control sites in all habitat types. Differences in vegetation structure are shown in Figure 2(a – f).

4.5.1.2 Botanical species composition

Winter wheat

In winter wheat, skylarks foraged in areas with significantly more bare ground (forage sites weighted mean $45.89\% \pm 6.69$ and control sites $29.03\% \pm 7.51$, $n = 7$) and significantly less winter wheat than in control areas (forage sites weighted mean $41.49\% \pm 6.57$ and control sites $57.80\% \pm 9.03$, $n = 7$) (Table 2 & Figure 3a).

Winter barley

Skylarks foraged in areas of winter barley with significantly more bare ground (forage sites weighted mean $57.11\% \pm 5.04$ and control sites $39.17\% \pm 6.70$, $n = 6$) and significantly less winter barley than control sites (forage sites weighted mean $31.50\% \pm 5.09$ and control sites $47.66\% \pm 5.91$, $n = 6$) (Table 3 and Figure 3f).

Beans

There was a significant year effect on the amount of bare ground and beans present in bean crops. More bare ground was present in 2001 (weighted mean $50.58\% \pm 6.23$, $n = 12$) than 2002 ($31.78\% \pm 35.82$, $n = 2$) and fewer beans were present in 2001 ($15.80\% \pm 4.24$) than 2002 ($55.52\% \pm 39.37$). There was also a significant difference in the amount of beans present in foraging and control quadrats with skylarks foraging in areas with

significantly less beans than control sites (Figure 2e). Although there was no effect of a year*quadrat type in beans there was a significant effect of year*quadrat type in perennial grasses (Table 4).

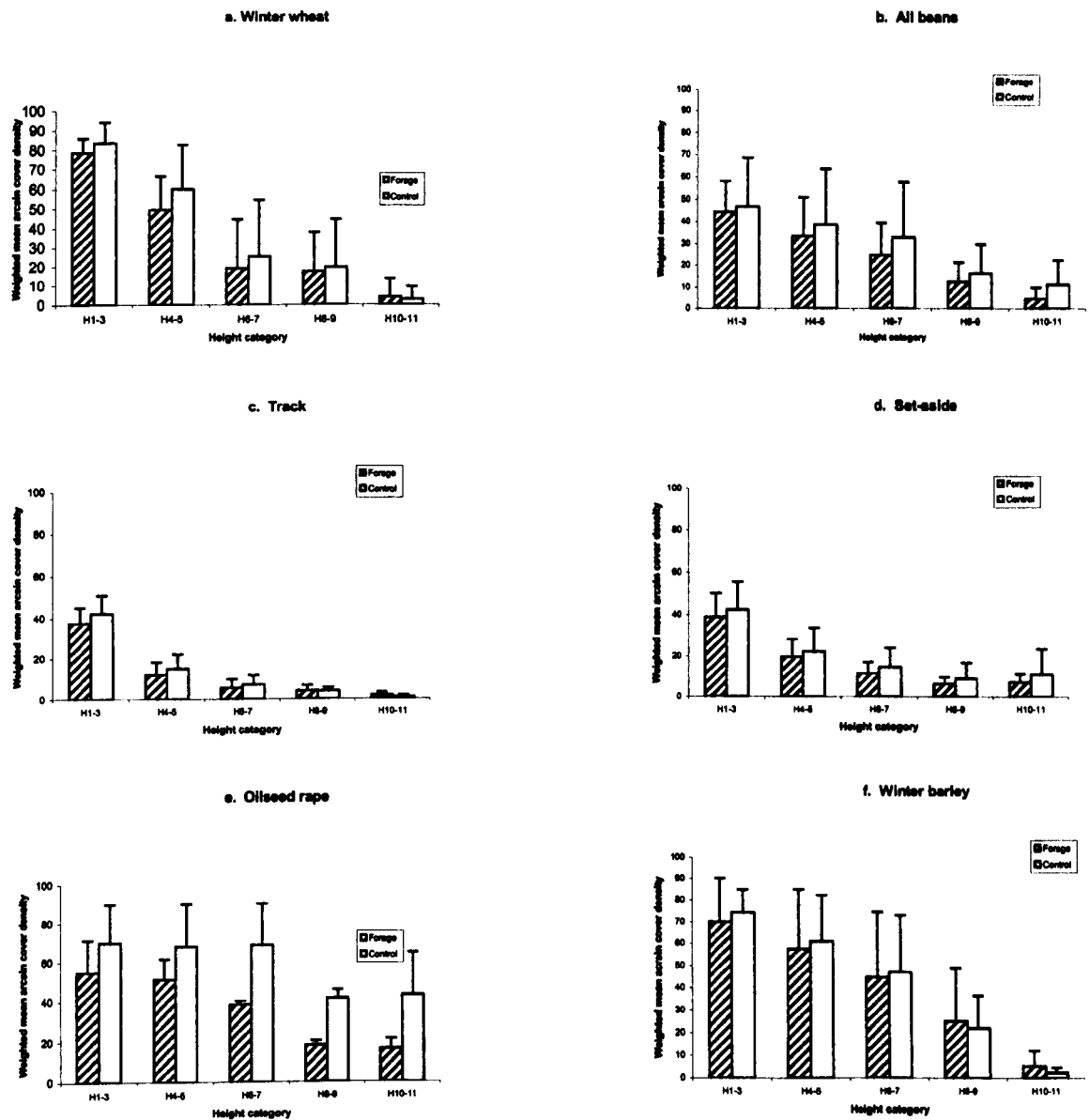


Figure 2: Vertical structure of skylark foraging and control sites within the specified foraging habitats. Weighted mean arcsin cover density presented, $\pm 1SE$. Pooled height categories represent vertical height of 0-20cm, 20-40cm, 40-60cm, 60-80cm and 80-100cm.

Table 2: Differences in vegetation composition between skylark foraging and control locations within winter wheat. All probabilities quoted within a single habitat type have been subjected to a sequential Bonferroni correction procedure to obtain table wide significance of $P < 0.05$ (Rice 1988). Figures in bold were significant before, and after, the Bonferroni correction was applied.

Vegetation type	Year	Quadrat type	Year * Quadrat type
<i>Bare ground</i>	$F_{(1,10)} = 1.58$ ns	$F_{(1,10)} = 18.32$ $P = 0.002$	$F_{(1,10)} = 0.60$ ns
<i>Winter wheat</i>	$F_{(1,10)} = 1.12$ ns	$F_{(1,10)} = 13.29$ $P = 0.004$	$F_{(1,10)} = 0.39$ ns
<i>All beans</i>	$F_{(1,10)} = 0.98$ ns	$F_{(1,10)} = 0.52$ ns	$F_{(1,10)} = 0.19$ ns
<i>Winter barley</i>	$F_{(1,10)} = 1.64$ ns	$F_{(1,10)} = 0.06$ ns	$F_{(1,10)} = 0.03$ ns
<i>Oilseed rape</i>	-	-	-
<i>Triticale</i>	-	-	-
<i>Perennial grasses</i>	$F_{(1,10)} = 4.31$ ns	$F_{(1,10)} = 0.05$ ns	$F_{(1,10)} = 0.526$ ns
<i>Annual grasses</i>	$F_{(1,10)} = 1.87$ ns	$F_{(1,10)} = 0.94$ ns	$F_{(1,10)} = 1.87$ ns
<i>Annual dicots</i>	$F_{(1,10)} = 0.11$ ns	$F_{(1,10)} = 0.37$ ns	$F_{(1,10)} = 0.02$ ns
<i>Perennial dicots</i>	-	-	-
<i>Biennial dicots</i>	-	-	-
<i>Other</i>	$F_{(1,10)} = 0.49$ ns	$F_{(1,10)} = 0.02$ ns	$F_{(1,10)} = 3.45$ ns

Table 3: Differences in vegetation composition between skylarks foraging and control locations within winter barley. All probabilities quoted within a single habitat type have been subjected to a sequential Bonferroni correction procedure to obtain table wide significance of $P < 0.05$ (Rice 1988). Figures in bold were significant before, and after, the Bonferroni correction was applied.

Vegetation type	Year	Quadrat type	Year * Quadrat type
<i>Bare ground</i>	$F_{(1,8)} = 4.75$ ns	$F_{(1,8)} = 36.31$ $P = 0.001$	$F_{(1,8)} = 0.10$ ns
<i>Winter wheat</i>	$F_{(1,8)} = 0.00$ ns	$F_{(1,8)} = 0.02$ ns	$F_{(1,8)} = 0.00$ ns
<i>All beans</i>	$F_{(1,8)} = 2.43$ ns	$F_{(1,8)} = 2.07$ ns	$F_{(1,8)} = 2.43$ ns
<i>Winter barley</i>	$F_{(1,8)} = 3.72$ ns	$F_{(1,8)} = 31.71$ $P = 0.001$	$F_{(1,8)} = 0.23$ ns
<i>Oilseed rape</i>	-	-	-
<i>Triticale</i>	-	-	-
<i>Perennial grasses</i>	$F_{(1,8)} = 0.10$ ns	$F_{(1,8)} = 0.16$ ns	$F_{(1,8)} = 0.01$ ns
<i>Annual grasses</i>	-	-	-
<i>Annual dicots</i>	$F_{(1,8)} = 0.57$ ns	$F_{(1,8)} = 0.26$ ns	$F_{(1,8)} = 0.00$ ns
<i>Perennial dicots</i>	$F_{(1,8)} = 0.00$ ns	$F_{(1,8)} = 0.03$ ns	$F_{(1,8)} = 2.17$ ns
<i>Biennial dicots</i>	-	-	-
<i>Other</i>	$F_{(1,8)} = 0.93$ ns	$F_{(1,8)} = 1.35$ ns	$F_{(1,8)} = 0.00$ ns

Table 4: Differences in vegetation composition between skylarks foraging and control locations within beans. All probabilities quoted within a single habitat type have been subjected to a sequential Bonferroni correction procedure to obtain table wide significance of $P < 0.05$ (Rice 1988). Figures in bold were significant before and after the Bonferroni correction was applied.

Vegetation type	Year	Quadrat type	Year * Quadrat type
<i>Bare ground</i>	$F_{(1,10)} = 7.28$ ns	$F_{(1,10)} = 2.74$ ns	$F_{(1,10)} = 2.73$, ns
<i>Winter wheat</i>	-	-	-
<i>All beans</i>	$F_{(1,10)} = 84.13$ $P = 0.001$	$F_{(1,10)} = 11.54$ $P = 0.007$	$F_{(1,10)} = 6.97$ ns
<i>Winter barley</i>	-	-	-
<i>Oilseed rape</i>	-	-	-
<i>Triticale</i>	-	-	-
<i>Perennial grasses</i>	$F_{(1,10)} = 0.64$ ns	$F_{(1,10)} = 11.56$ ns	$F_{(1,10)} = 12.43$ $P = 0.005$
<i>Annual grasses</i>	-	-	-
<i>Annual dicots</i>	$F_{(1,10)} = 4.64$ ns	$F_{(1,10)} = 0.2$ ns	$F_{(1,10)} = 0.00$, ns
<i>Perennial dicots</i>	$F_{(1,10)} = 4.02$ ns	$F_{(1,10)} = 0.88$ ns	$F_{(1,10)} = 0.32$, ns
<i>Biennial dicots</i>	$F_{(1,10)} = 0.77$ ns	$F_{(1,10)} = 2.89$ ns	$F_{(1,10)} = 7.86$, ns
<i>Other</i>	$F_{(1,10)} = 0.09$ ns	$F_{(1,10)} = 6.75$ ns	$F_{(1,10)} = 1.53$, ns

Oilseed rape

Only two skylark pairs foraged in oilseed rape: one in 2001 and one in 2002. Data was not analysed but there was a trend for foraging sites to contain more bare ground and less oilseed rape than control sites (Figure 3b).

Set-aside

There was a significant year effect in the amount of bare ground and perennial dicotyledons found in 2001 and 2002 although there was no difference in the vegetation composition between foraging and control quadrats (Figure 2c and Table 5). In 2001 there was less bare ground present than in 2002, with a weighted mean of $32.62\% \pm 5.26$, $n = 26$ and $55.80\% \pm 12.91$, $n = 10$ respectively.

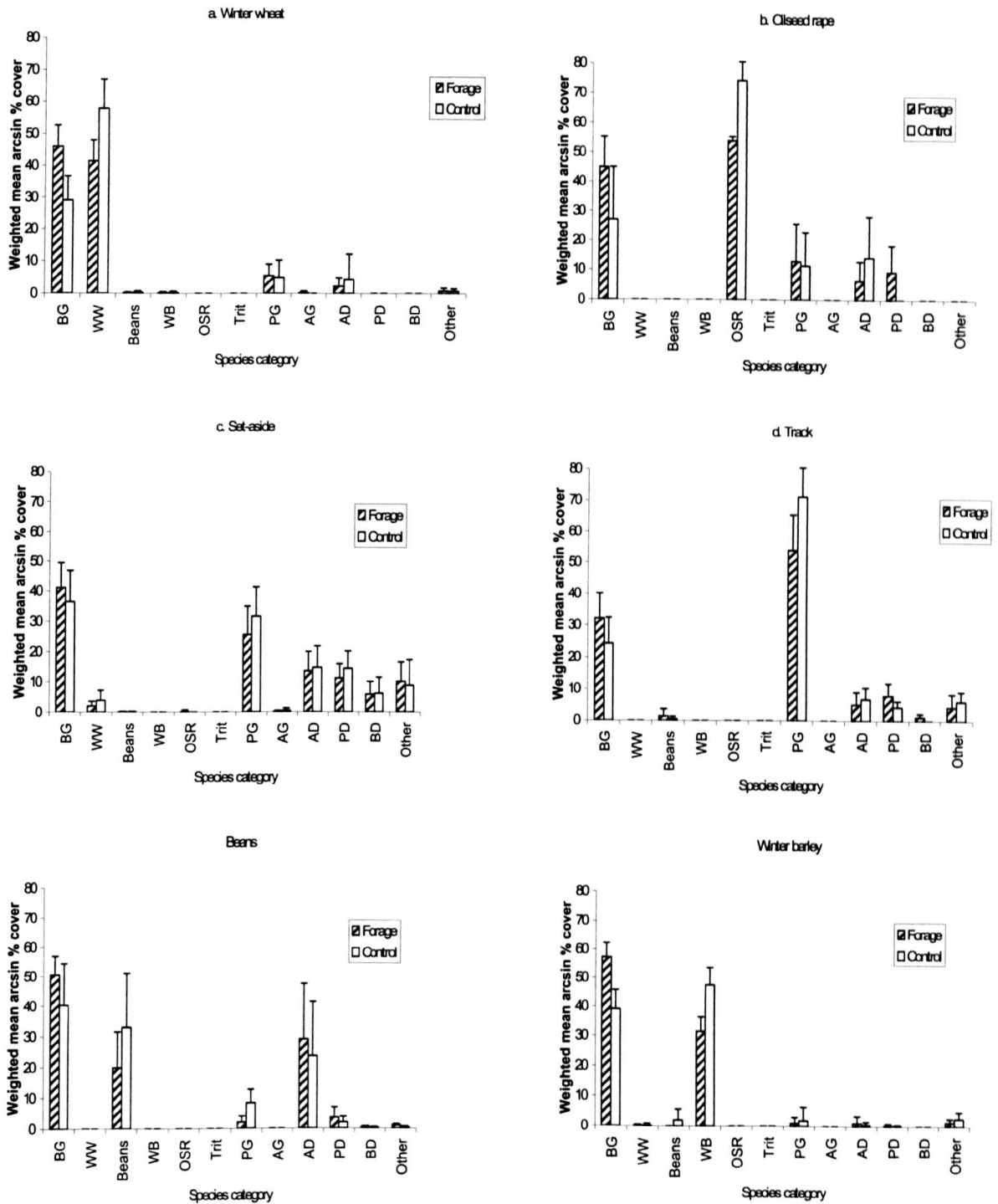


Figure 3: Weighted mean percentage cover of botanical species groups represented ± 1 SE at skylark foraging and control sites in the various habitat categories available. Categories represented; Bare ground (BG) Winter wheat (WW), Beans, Winter barley (WB), Oilseed rape (OSR), Triticale (Trit), Perennial grasses (PG), Annual grasses (AG), Annual dicotyledons (AD), Perennial dicotyledons (PD), Biennial dicotyledons (BD), Other species (Other).

Table 5: Differences in vegetation composition between skylarks foraging and control locations within set-aside (all types). All probabilities quoted within a single habitat type have been subjected to a sequential Bonferonni correction procedure to obtain table wide significance of $P < 0.05$ (Rice 1988). Figures in bold were significant before, and after, the Bonferroni correction was applied.

Vegetation type	Year	Quadrat type	Year * Quadrat type
<i>Bare ground</i>	$F_{(1,32)} = \mathbf{23.65}$ $P = \mathbf{0.001}$	$F_{(1,32)} = 1.21$ ns	$F_{(1,32)} = 0.92$ ns
<i>Winter wheat</i>	$F_{(1,32)} = 7.00$ ns	$F_{(1,32)} = 1.93$ ns	$F_{(1,32)} = 0.70$ ns
<i>All beans</i>	$F_{(1,32)} = 1.64$ ns	$F_{(1,32)} = 0.03$ ns	$F_{(1,32)} = 0.01$ ns
<i>Winter barley</i>	-	-	-
<i>Oilseed rape</i>	$F_{(1,32)} = 0.41$ ns	$F_{(1,32)} = 1.13$ ns	$F_{(1,32)} = 0.41$ ns
<i>Triticale</i>	-	-	-
<i>Perennial grasses</i>	$F_{(1,32)} = 5.82$ ns	$F_{(1,32)} = 1.30$ ns	$F_{(1,32)} = 0.12$ ns
<i>Annual grasses</i>	$F_{(1,32)} = 0.67$ ns	$F_{(1,32)} = 1.01$ ns	$F_{(1,32)} = 0.03$ ns
<i>Annual dicots</i>	$F_{(1,32)} = 1.05$ ns	$F_{(1,32)} = 0.07$ ns	$F_{(1,32)} = 0.10$, ns
<i>Perennial dicots</i>	$F_{(1,32)} = \mathbf{28.38}$ $P = \mathbf{0.001}$	$F_{(1,32)} = 1.99$ ns	$F_{(1,32)} = 0.90$, ns
<i>Biennial dicots</i>	$F_{(1,32)} = 0.77$ ns	$F_{(1,32)} = 0.01$ ns	$F_{(1,32)} = 0.09$, ns
<i>Other</i>	$F_{(1,32)} = 3.16$ ns	$F_{(1,32)} = 0.10$ ns	$F_{(1,32)} = 0.81$, ns

Track

There was a significant year effect in the amount of biennial dicotyledons found in 2001 and 2002 with more biennial dicotyledons present in 2002 (weighted mean $1.96\% \pm 2.07$, $n = 4$) than 2001 ($0.81\% \pm 1.75$, $n = 10$). There was no significant difference in the vegetation compositions between foraging and control quadrats (Table 6), but for biennial dicotyledons a significant year+quadrat effect was found.

4.5.1.3 Botanical species richness

There was no significant difference in plant species richness found at skylark foraging or control sites in any of the foraging habitat categories (Table 7). However there were significant differences in the number of species found between years in winter wheat (mean number of species 2001 = 2.32 ± 0.25 , $n = 8$, 2002 = 3.63 ± 0.78 , $n=6$), set-aside (mean number of species 2001 = 4.82 ± 0.42 , $n = 26$, 2002 = 3.36 ± 0.56 , $n=10$) and beans (mean number of species 2001 = 2.45 ± 0.31 , $n = 8$, 2002 = 3.39 ± 1.42 , $n=4$).

Table 6: Differences in vegetation composition between skylarks foraging and control locations on tracks. All probabilities quoted within a single habitat type have been subjected to a sequential Bonferroni correction procedure to obtain table wide significance of $P < 0.05$ (Rice 1988). Figures in bold were significant before, and after, the Bonferroni correction was applied.

Vegetation type	Year	Quadrat type	Year * Quadrat type
<i>Bare ground</i>	$F_{(1,12)} = 0.27$ ns	$F_{(1,12)} = 0.69$ ns	$F_{(1,12)} = 0.11$ ns
<i>Winter wheat</i>	-	-	-
<i>All beans</i>	$F_{(1,12)} = 0.38$ ns	$F_{(1,12)} = 0.19$ ns	$F_{(1,12)} = 0.08$ ns
<i>Winter barley</i>	-	-	-
<i>Oilseed rape</i>	-	-	-
<i>Triticale</i>	-	-	-
<i>Perennial grasses</i>	$F_{(1,12)} = 0.15$ ns	$F_{(1,12)} = 1.93$ ns	$F_{(1,12)} = 0.15$ ns
<i>Annual grasses</i>	-	-	-
<i>Annual dicots</i>	$F_{(1,12)} = 1.15$ ns	$F_{(1,12)} = 0.15$ ns	$F_{(1,12)} = 0.08$ ns
<i>Perennial dicots</i>	$F_{(1,12)} = 5.81$ ns	$F_{(1,12)} = 1.48$ ns	$F_{(1,12)} = 1.39$ ns
<i>Biennial dicots</i>	$F_{(1,12)} = 12.46$ $P = 0.004$	$F_{(1,12)} = 5.54$ ns	$F_{(1,12)} = 12.46$ $P = 0.004$
<i>Other</i>	$F_{(1,12)} = 0.01$ ns	$F_{(1,12)} = 0.17$ ns	$F_{(1,12)} = 0.41$ ns

Table 7: Weighted mean number of botanical species found in skylark foraging and control locations within the different foraging habitats during 2001 and 2002, ± 1 SE.

Habitat category	Mean number of plant species (± 1 SE)		Significance	
	Foraging site	Control site	Year	Quadrat type
<i>Winter wheat</i>	3.08 ± 0.82	3.30 ± 0.80	$t_{(12)} = 4.34$, $P = 0.001$	$t_{(12)} = 4.90$, ns
<i>Winter barley</i>	2.95 ± 0.75	2.62 ± 0.39	$t_{(10)} = 1.14$, ns	$t_{(10)} = 0.00$, ns
<i>Beans</i>	2.52 ± 0.40	2.87 ± 0.83	$t_{(8)} = 2.81$, $P = 0.023$	$t_{(8)} = 0.89$, ns
<i>Set-aside</i>	4.41 ± 0.63	4.45 ± 0.60	$t_{(34)} = 4.65$, $P < 0.001$	$t_{(34)} = 0.10$, ns
<i>Track</i>	4.12 ± 0.65	3.56 ± 0.53	$t_{(14)} = 0.57$, ns	$t_{(14)} = 0.82$, ns

4.5.2 Comparison between skylark and yellowhammer foraging sites in 2000

4.5.2.1 *Vegetation structure at foraging sites*

There were no significant differences in vertical height structure between skylark and yellowhammer foraging sites in any of the foraging habitat types although there was a trend for yellowhammers to forage in areas with taller denser vegetation in each habitat type in the higher height categories apart from oilseed rape (Figure 4).

4.5.2.2 *Botanical species composition*

There were no significant differences between the percentage cover of any of the vegetation types at skylark and yellowhammer foraging locations within winter wheat or oilseed rape (Table 8, Figure 5 a,b). On tracks skylarks foraged in areas with significantly more perennial grasses than yellowhammers did (Figure 5d). Skylarks also foraged in areas with significantly more bare ground in winter beans (Figure 5e) and less oilseed rape or kale cover in set-aside than yellowhammers did (Figure 5c). However, after a bonferroni correction was applied, only the amount of oilseed rape in set-aside was significantly different between the two species foraging sites within the same habitat type. In 2000, skylarks were never recorded foraging in winter barley, unlike the yellowhammer.

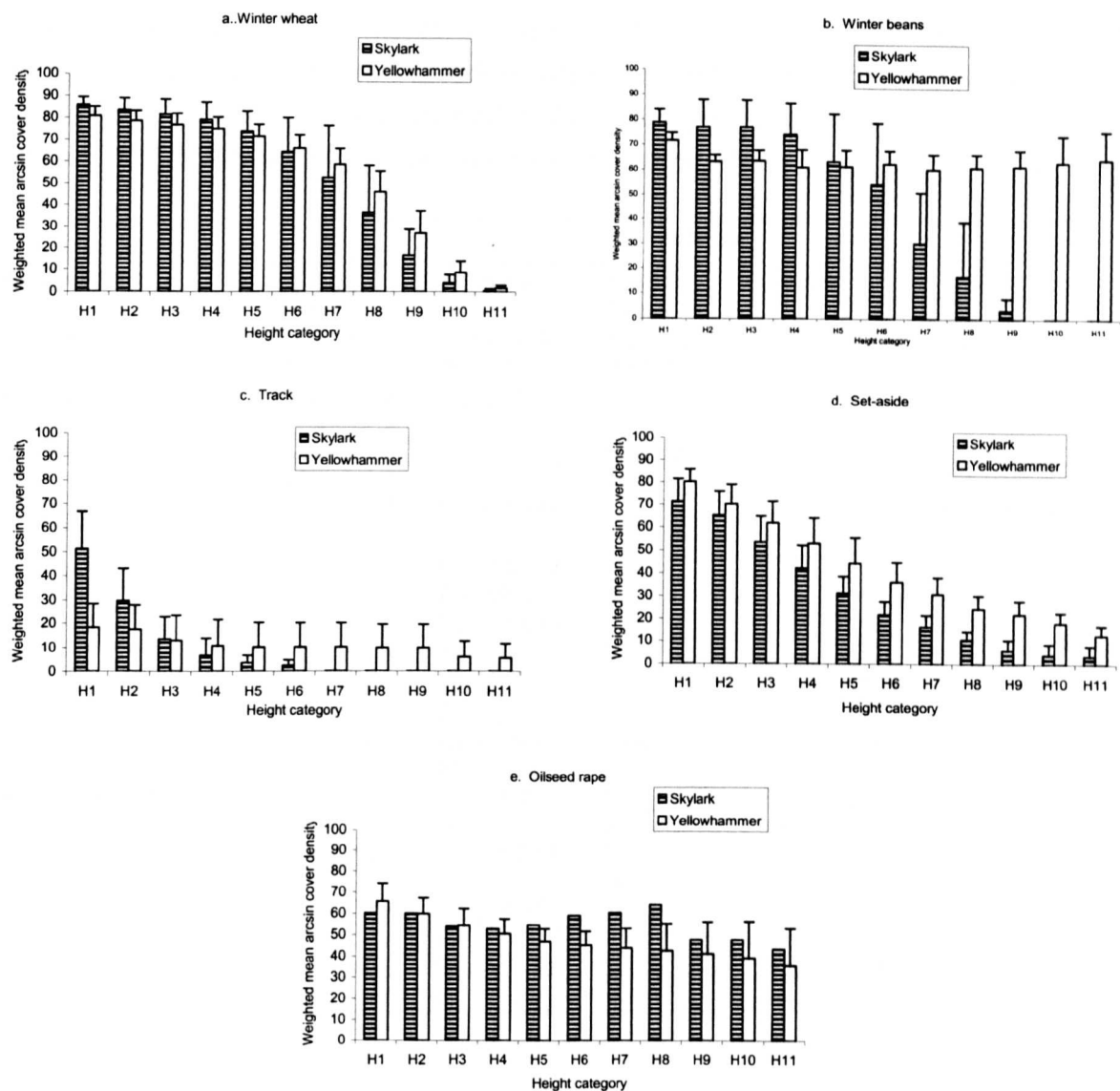


Figure 4: Vertical height structure at skylark and yellowhammer foraging sites within the specified foraging habitats. Weighted mean arcsin cover density presented, ± 1 SE, at each of the 11 height categories.

Table 8: Differences in vegetation composition between skylarks and yellowhammers at foraging locations within winter wheat, set-aside, winter beans, track and oilseed rape. All probabilities quoted within a single habitat type have been subjected to a sequential Bonferonni correction procedure to obtain table wide significance of $P < 0.05$ (Rice 1988) and significant values are presented in bold.

Vegetation type	Habitat type				
	Winter Wheat	Set Aside	Winter Beans	Track	Oilseed Rape
<i>Bare ground</i>	$F_{(1,18)} = 0.46$, ns	$F_{(1,15)} = 0.33$, ns	$F_{(1,3)} = 11.02$, $P = 0.045$, ns	$F_{(1,4)} = 0.360$, ns	$F_{(1,5)} = 1.08$, ns
<i>Winter wheat</i>	$F_{(1,18)} = 0.00$, ns	$F_{(1,15)} = 0.61$, ns	-	-	-
<i>Winter beans</i>	$F_{(1,18)} = 0.07$, ns	-	$F_{(1,3)} = 2.58$, ns	-	-
<i>Winter barley</i>	$F_{(1,18)} = 0.37$, ns	$F_{(1,15)} = 0.81$, ns	-	-	$F_{(1,5)} = 0.28$, ns
<i>Oilseed rape</i>	-	$F_{(1,15)} = 15.58$, $P = 0.001$	-	-	$F_{(1,5)} = 1.58$, ns
<i>Triticale</i>	-	$F_{(1,15)} = 3.49$, ns	-	-	-
<i>Perennial grasses</i>	$F_{(1,18)} = 0.36$, ns	$F_{(1,15)} = 0.01$, ns	-	$F_{(1,4)} = 14.34$, $p = 0.019$, ns	$F_{(1,5)} = 1.14$, ns
<i>Annual grasses</i>	$F_{(1,18)} = 2.84$, ns	$F_{(1,15)} = 0.17$, ns	$F_{(1,3)} = 0.50$, ns	$F_{(1,4)} = 0.10$, ns	-
<i>Annual dicotyledons</i>	$F_{(1,18)} = 0.79$, ns	$F_{(1,15)} = 0.67$, ns	$F_{(1,3)} = 1.67$, ns	$F_{(1,4)} = 0.72$, ns	$F_{(1,5)} = 0.71$, ns
<i>Perennial dicotyledons</i>	$F_{(1,18)} = 0.69$, ns	$F_{(1,15)} = 2.57$, ns	$F_{(1,3)} = 1.21$, ns	-	$F_{(1,5)} = 1.66$, ns
<i>Biennial dicotyledons</i>	-	$F_{(1,15)} = 0.60$, ns	-	-	-
<i>Others</i>	$F_{(1,18)} = 0.01$, ns	$F_{(1,15)} = 0.82$, ns	$F_{(1,3)} = 3.04$, ns	$F_{(1,4)} = 1.00$, ns	-

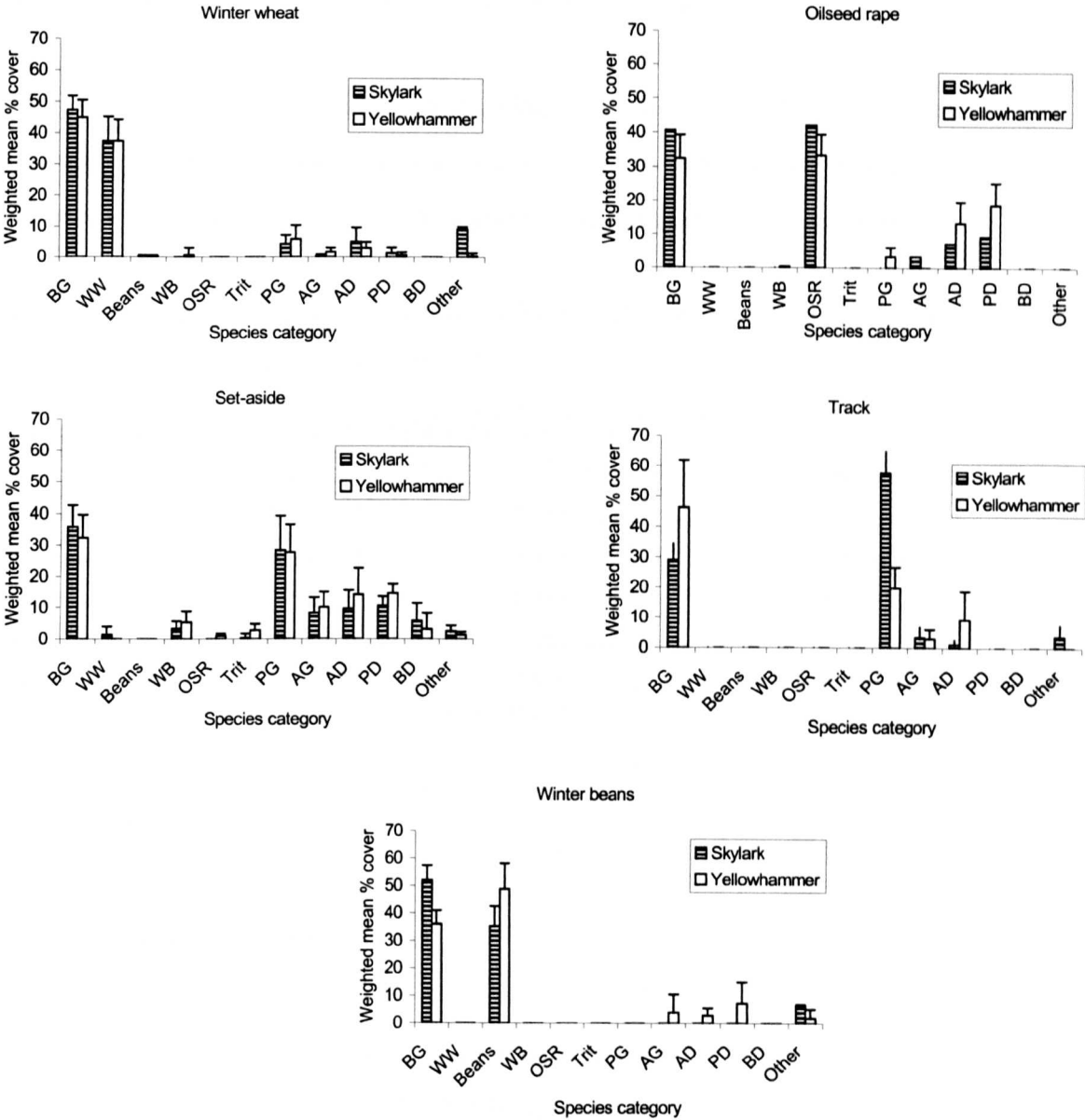


Figure 5: The weighted mean percentage cover differences, ± 1 SE, of bare ground (BG), winter wheat (WW), Beans, winter barley (WB), oilseed rape (OSR), triticale (Trit), perennial grasses (PG), annual grasses (AG), annual dicotyledons (AD), perennial dicotyledons (PD) and other species (Other) within the same habitat type by foraging skylarks and yellowhammers.

4.5.2.3 Botanical species richness at skylark and yellowhammer foraging sites

There was no significant difference in the number of plant species found at skylark or yellowhammer foraging sites in any of the foraging habitat categories (Table 9). Only one skylark pair foraged in oilseed rape compared to six yellowhammer pairs, and 2 skylarks and 3 yellowhammer pairs in winter beans.

Table 9: Weighted mean number of botanical species found in different skylark and yellowhammer foraging locations within the different foraging habitats, \pm 1SE.

Foraging habitat	Mean number plant species (\pm 1SE)		Significance
	Skylark	Yellowhammer	
Winter wheat	1.78 (\pm 0.43)	1.55 (\pm 0.31)	$t_{(18)} = 0.93$, ns
Winter beans	1.50 (\pm 0.32)	1.93 (\pm 0.77)	$t_{(3)} = 0.66$, ns
Oilseed rape	2.17 (\pm 2.17)	2.68 (\pm 0.45)	$t_{(5)} = 0.96$, ns
Set-aside	4.13 (\pm 0.58)	3.65 (\pm 0.55)	$t_{(15)} = 0.98$, ns
Track	2.00 (\pm 1.00)	1.50 (\pm 0.29)	$t_{(4)} = 0.48$, ns

4.5.3 Song thrushes

4.5.3.1 Vegetation cover density

For provisioning birds, cover density data from 19 nests were collected; 117 cover density boards from 11 nests in 2001 and 71 boards from 8 nests in 2002. Data from 60 cover density boards were also collected from 4 birds with no nest attempts in 2001 (from within the home range after at least 30 fixes were collected).

4.5.3.1.1 Vegetation structure differences between foraging and control sites

Data were analysed using 119 boards, 48 from 5 nests in 2001 and 71 from 8 nests in 2002. Data from so few nests were available because in 2001 control samples were not taken after mid-June and in 2002 data from 8 nests only were collected.

Initial analysis showed that the effect of nest nested within year was significantly different for each habitat type tested apart from woodland, so the mean of paired differences for each nest was calculated and tested for a year effect, which was not significant. Repeated measures analysis testing for differences in vertical height categories between song thrush foraging and control sites found no significant differences in any of the habitat types (Table 10).

Table 10: Vertical vegetation structure differences between song thrush foraging and control sites in woodland, grass habitats (permanent pasture, grass track and garden), boundary and boundary+tall herbaceous vegetation habitat categories. (Yr = year, Ht = height).

Habitat type	Paired differences (all data)	Mean paired differences per nest	Repeated measures analysis
	<i>Nested anova</i>	<i>Year effect</i>	<i>Ht differences</i>
<i>Woodland</i>	Yr: $\lambda = 0.967$, $F_{(5,24)} = 0.16$, ns Yr.Nest: $\lambda = 0.241$, $F_{(50,113)} = 0.83$, ns	$\lambda = 0.986$, $F_{(5,34)} = 0.10$, ns	Ht: $\lambda = 0.626$, $F_{(4,7)} = 1.05$, ns Ht.Year: $\lambda = 0.927$, $F_{(4,7)} = 0.14$, ns
<i>Grass habitats</i>	Yr: $\lambda = 0.148$, $F_{(4,9)} = 12.97$, $P < 0.001$ Yr.Nest: $\lambda = 0.004$, $F_{(16,28)} = 9.07$, $P < 0.001$	$\lambda = 0.492$, $F_{(4,2)} = 0.52$, ns	Ht: $\lambda = 0.791$, $F_{(3,3)} = 0.26$, ns Ht.Year: $\lambda = 0.592$, $F_{(3,3)} = 0.69$, ns
<i>Boundary</i>	Yr: $\lambda = 0.790$, $F_{(5,23)} = 1.22$, ns Yr.Nest: $\lambda = 0.042$, $F_{(40,103)} = 2.77$, $P < 0.001$	$\lambda = 0.685$, $F_{(5,4)} = 0.37$, ns	Ht: $\lambda = 0.831$, $F_{(4,5)} = 0.25$, ns Ht.Year: $\lambda = 0.857$, $F_{(4,5)} = 0.21$, ns
<i>Boundary+tall herbaceous vegetation</i>	Yr: $\lambda = 0.840$, $F_{(5,28)} = 1.07$, ns Yr.Nest: $\lambda = 0.079$, $F_{(45,128)} = 2.18$, $P < 0.001$	$\lambda = 0.723$, $F_{(5,7)} = 0.54$, ns	Ht: $\lambda = 0.873$, $F_{(4,8)} = 0.29$, ns Ht.Year: $\lambda = 0.799$, $F_{(4,8)} = 0.51$, ns

4.5.3.1.2 Vegetation structure at foraging sites within the provisioning range and the home range

Data were analysed from 132 cover density boards, 72 from the foraging range of 6 nests and 60 from the home range of 4 nests. All data for this analysis in 2001 were collected during mid-June, July and August and

no control data were taken during this period. Home range and forage range vegetation data were compared with one another to see whether vegetation height structure differed when birds were provisioning young or not.

For the purpose of this analysis habitat categories permanent pasture+grass and track+mown grass in gardens were combined to form a 'grass habitat' category. Boundary and tall herbaceous vegetation data were combined to form a boundary+tall herbaceous vegetation category. Woodland vegetation structure within the two types of ranges was also compared. There were insufficient data in terms of number of nests to investigate differences in vegetation structure within cereal and broadleaved crop habitat types.

There was no significant difference in the vegetation structure in boundary+tall herbaceous vegetation, grass habitats and boundary (when analysed alone). Woodland showed differences in month ($\lambda = 0.001$, $F_{(5,1)} = 316.67$, $P = 0.043$) but not in range categories ($\lambda = 0.030$, $F_{(5,1)} = 6.39$, ns) between foraging range and home range samples, with June having more dense vegetation (overall average $57.04\% \pm 4.58$) than July (overall average $52.82\% \pm 5.88$) across all height categories.

4.5.4 Invertebrate abundance at foraging sites

4.5.4.1 Skylarks

There was no effect of year on the paired differences (forage-control). There were no significant differences in weighted mean invertebrate abundance of any of the invertebrate groups between skylark foraging and control sites in any of the habitat categories, or in total invertebrate abundance.

4.5.4.2 Skylark vs yellowhammer

Overall there were significantly more invertebrates found at skylark foraging sites compared to yellowhammer foraging sites in winter wheat but no difference in invertebrate abundance in set-aside. There were significantly more araneae, aphids, other coleoptera and other insects at skylark foraging sites in winter wheat

when compared to yellowhammers. However, after the Bonferroni correction was applied the only true significant difference was in the abundance of araneae, with more being present in skylark than yellowhammer foraging sites (Table 11). Figure 6 shows a graphical representation of the data.

Table 11: Mean invertebrate abundance found at skylark and yellowhammer foraging sites in set-aside and winter wheat, \pm 1SE. Only P-values in bold remain significant after a Bonferroni correction factor was applied to $\ln(x+1)$ transformed data used in the analysis (see text).

<i>Invertebrate Group</i>	Set-aside			Winter wheat		
	<i>SL mean</i>	<i>YH mean</i>	<i>F-value</i>	<i>SL mean</i>	<i>YH mean</i>	<i>F-value</i>
<i>Araneae</i>	1.83 \pm 0.36	0.46 \pm 0.16	$F_{(1,8)} = 4.54$, ns	2.06 \pm 0.23	0.74 \pm 0.15	$F_{(1,14)} = 20.65$, $P < 0.001$
<i>Other arthropods</i>	0.00 \pm 0.00	0.79 \pm 0.79	$F_{(1,8)} = 1.99$, ns	0.09 \pm 0.03	0.30 \pm 0.11	$F_{(1,14)} = 1.98$, ns
<i>Other insects</i>	2.78 \pm 0.46	4.61 \pm 1.00	$F_{(1,8)} = 1.08$, ns	10.24 \pm 1.25	3.28 \pm 0.60	$F_{(1,14)} = 14.76$, $P = 0.02$, ns
<i>Homoptera</i>	3.28 \pm 0.93	0.86 \pm 0.20	$F_{(1,8)} = 1.32$, ns	3.03 \pm 0.55	3.04 \pm 0.72	$F_{(1,14)} = 0.00$, ns
<i>Other hemiptera</i>	1.67 \pm 0.49	0.68 \pm 0.21	$F_{(1,8)} = 0.75$, ns	1.25 \pm 0.20	1.32 \pm 0.35	$F_{(1,14)} = 0.18$, ns
<i>Aphidae</i>	1.22 \pm 0.27	16.89 \pm 12.11	$F_{(1,8)} = 9.14$, $P = 0.016$, ns	5.22 \pm 0.53	2.92 \pm 0.50	$F_{(1,14)} = 5.81$, $P = 0.030$, ns
<i>Lepidoptera</i>	0.09 \pm 0.04	0.00 \pm 0.00	$F_{(1,8)} = 0.88$, ns	0.04 \pm 0.02	0.06 \pm 0.03	$F_{(1,14)} = 0.06$, ns
<i>Hymenoptera</i>	0.07 \pm 0.04	0.04 \pm 0.04	$F_{(1,8)} = 0.20$, ns	0.04 \pm 0.02	0.06 \pm 0.04	$F_{(1,14)} = 0.01$, ns
<i>Other hymenoptera</i>	15.89 \pm 2.30	13.32 \pm 2.07	$F_{(1,8)} = 0.00$, ns	22.20 \pm 1.72	12.80 \pm 1.12	$F_{(1,14)} = 0.69$, ns
<i>Coleoptera</i>	6.30 \pm 0.80	8.64 \pm 1.36	$F_{(1,8)} = 2.68$, ns	12.63 \pm 0.72	10.30 \pm 0.99	$F_{(1,14)} = 3.23$, ns
<i>Other coleoptera</i>	4.02 \pm 0.47	7.04 \pm 1.70	$F_{(1,8)} = 0.12$, ns	2.87 \pm 0.461	1.33 \pm 0.30	$F_{(1,14)} = 4.71$, $P = 0.048$, ns
<i>Diptera</i>	1.02 \pm 0.30	1.71 \pm 0.45	$F_{(1,8)} = 1.56$, ns	7.44 \pm 0.74	4.69 \pm 0.72	$F_{(1,14)} = 0.79$, ns
<i>Other diptera</i>	13.72 \pm 2.12	31.14 \pm 7.02	$F_{(1,8)} = 4.59$, ns	26.00 \pm 2.020	12.74 \pm 1.68	$F_{(1,14)} = 2.53$, ns
<i>Total invertebrates</i>	51.89 \pm 5.12	86.18 \pm 14.35	$F_{(1,8)} = 4.34$, ns	93.11 \pm 4.69	52.69 \pm 4.08	$F_{(1,14)} = 10.44$, $P = 0.006$, ns

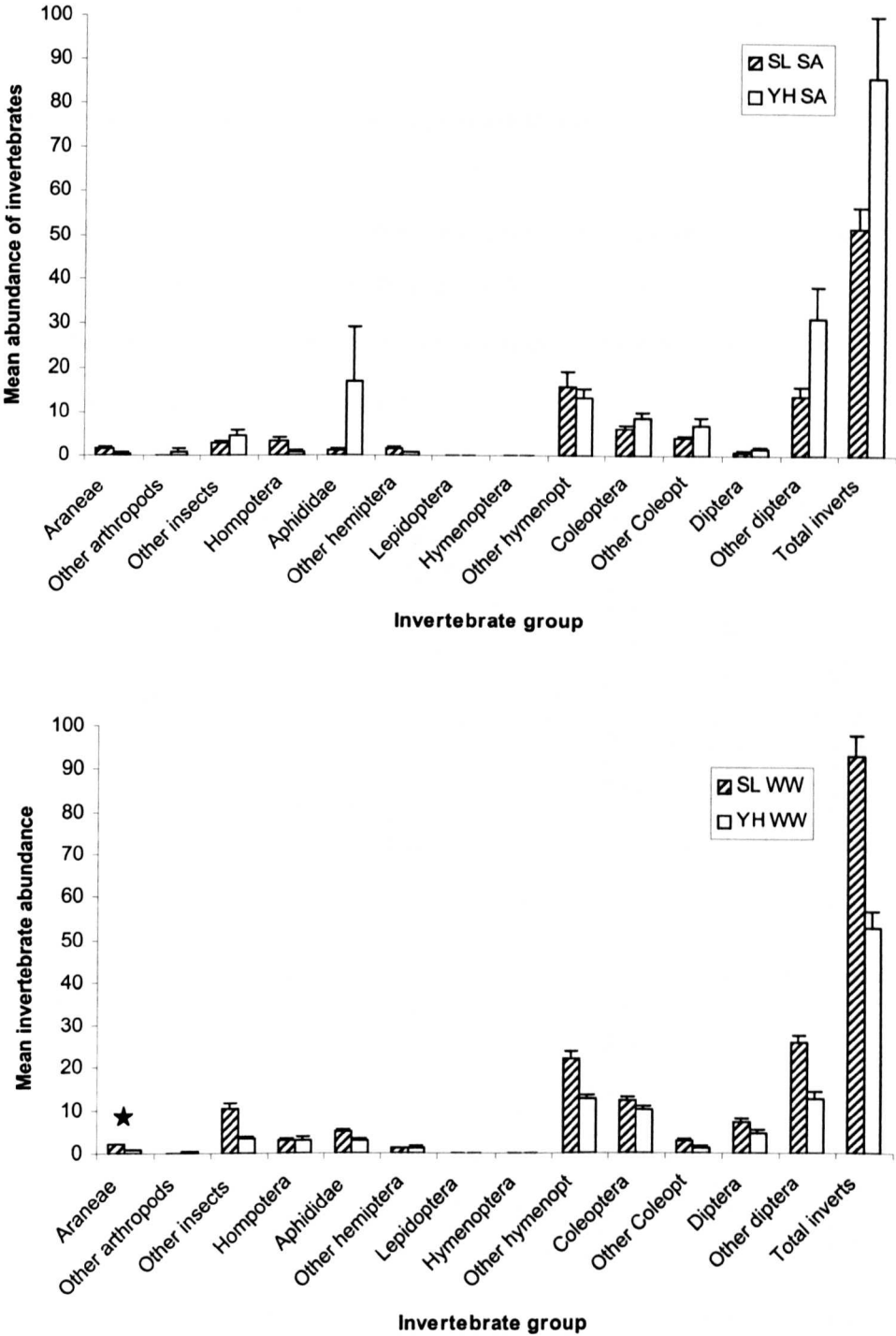


Figure 6: Mean abundance of different invertebrate groups found in skylark (SL) and yellowhammer (YH) foraging sites in winter wheat (WW) and set-aside (SA), \pm 1SE. ★ Signifies a significant difference after Bonferroni correction using $\ln(x+1)$ transformed data in the analysis (section 4.5.4.2).

4.5.4.3 Song thrush worm samples

4.5.4.3.1 Foraging vs control sites within the provisioning range

Analysis took place at three levels; the total invertebrate weight, total worm weight and total slug and snail weight. At each level, no significant difference was detected between year or foraging and control cores in any of the habitat types, although there appeared to be more invertebrates present in foraging than control sites in grass habitats, wood and boundary (Figure 7).

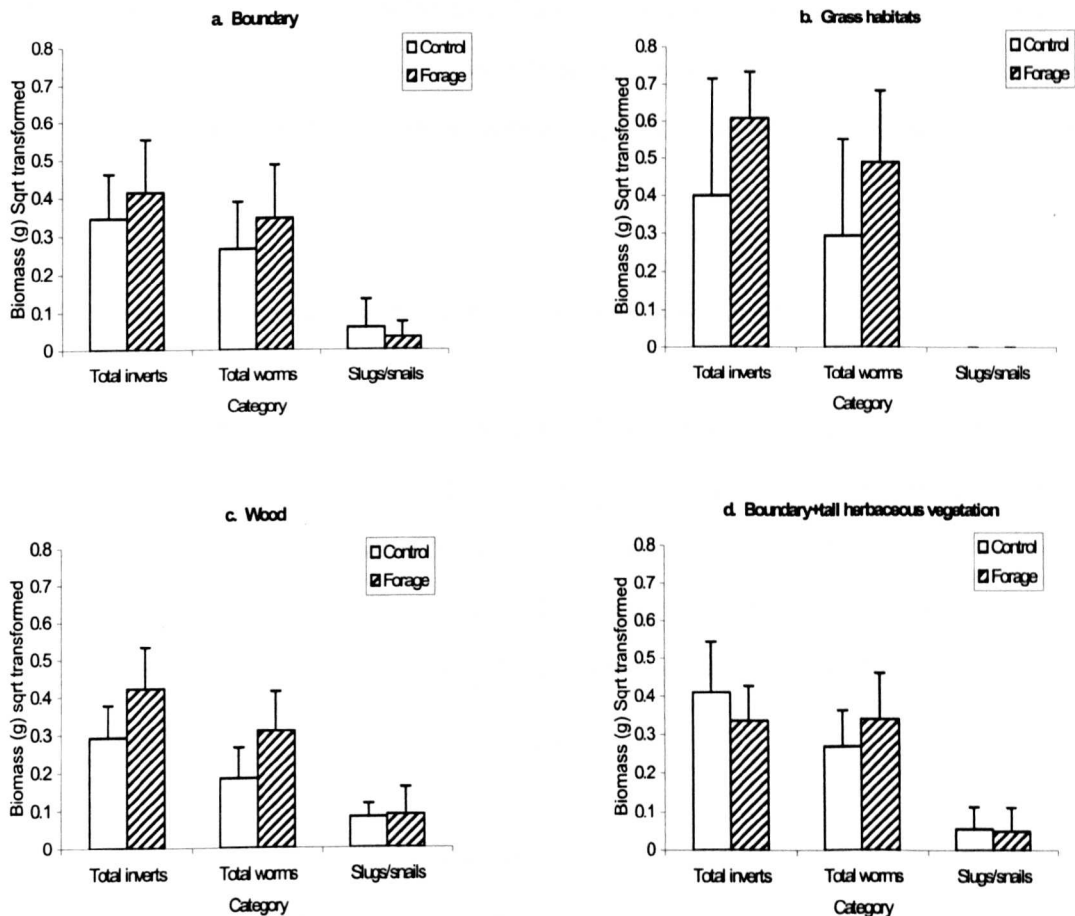


Figure 7: Weighted mean earthworm, 'total invertebrates' and slug and snail biomass, square root transformed \pm 1 SE, in four song thrush foraging habitats. Grass habitats include cores taken from gardens, pasture and grass tracks, wood includes cores taken within new and established woodland and boundary includes cores taken from hedges, ditches, verges and field margins. Forage – data from soil cores at foraging sites within the provisioning range, Control – data from soil cores at non-foraging sites within the provisioning range.

4.5.4.3.2 Comparison of invertebrates found at song thrush foraging sites between the provisioning and home ranges

Invertebrate foraging samples taken after mid-June in 2001 from provisioning ranges were compared with invertebrate samples taken from home ranges in 2001 in wood, boundary, boundary+tall herbaceous vegetation, grass habitats and broadleaved crop habitat types. Data from 132 soil cores were used in the analysis. No control soil cores were available for either of these time periods.

There was a significant difference in the total worm weight in 'boundary' habitat ($F_{(1,5)} = 8.40$, $P = 0.034$) between foraging and home range soil cores but no difference in month ($F_{(2,8)} = 1.78$, $P = 0.229$) (Figure 8). Lower earthworm and total invertebrate biomass were found within the provisioning range of birds feeding nestlings. No other habitats showed any significant difference in invertebrate abundance between provisioning and home range samples.

4.5.4.3.2 Differences in invertebrate abundance between foraging habitat types

Foraging and control samples for each nest were combined since no differences were found in invertebrate or worm biomass between song thrush foraging and control sites. Further analysis was performed to investigate whether there were any differences in worm biomass or total invertebrate biomass between habitat types. ANOVA was used to test for year, nest and then habitat type effects and the dependent variable was invertebrate or worm biomass. The number of soil cores taken per nest per habitat type was used as a weighting variable in the analysis.

Year and nest had no significant effect for each analysis type. There was no significant difference in worm biomass between foraging habitat types but there was a significant difference in total invertebrate biomass ($F_{(5,32)} = 2.71$, $P = 0.037$). Figure 9 shows that boundary, grass, tall herbaceous and woodland habitats had greater worm and invertebrate biomass than cereals and broadleaved crops.

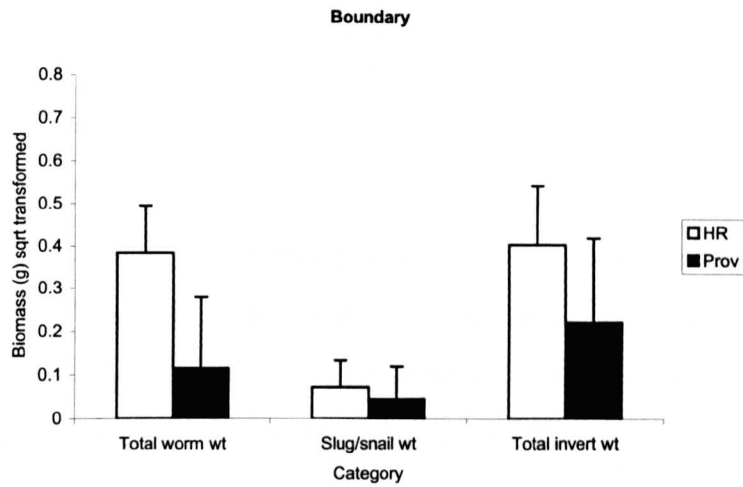


Figure 8: Weighted mean of 'all invertebrates', slug and snail and total invertebrate biomass, square root transformed \pm 1SE, in boundary song thrush foraging habitats within the foraging and home range. Boundary includes cores taken from hedges, ditches, verges and field margins. HR = home range (i.e. birds foraging for themselves), Prov = foraging range (i.e. birds provisioning young).

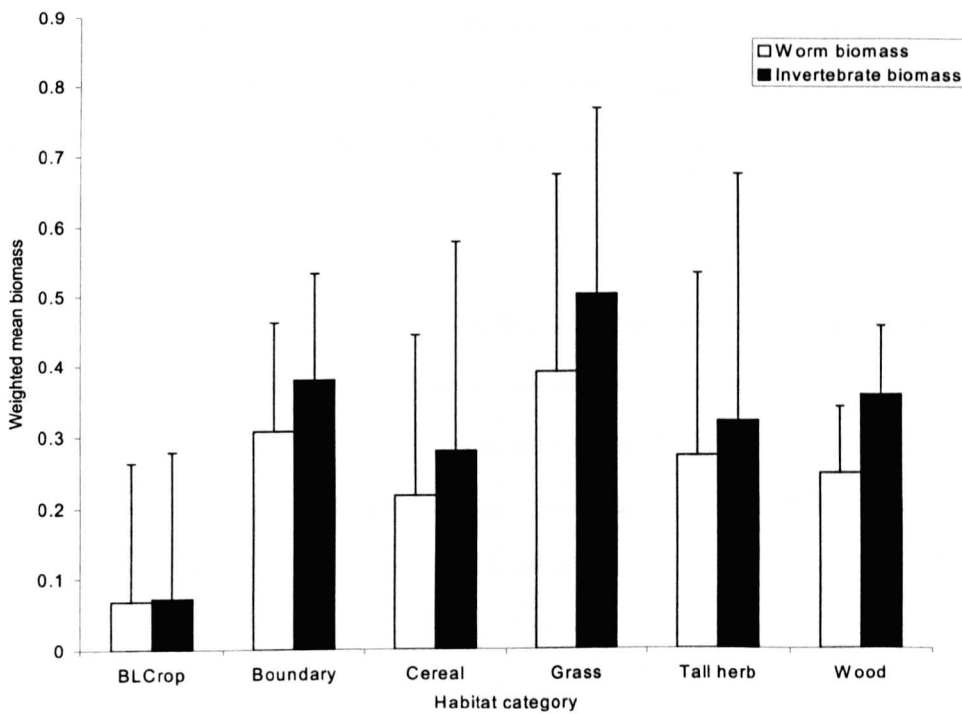


Figure 9: Weighted mean biomass of worm and total invertebrates, \pm 1SE, within song thrush foraging habitat types. Foraging and control soil cores were combined. See text for habitat category explanations.

4. 6 Discussion

4.6.1 Skylarks

Results of this study found limited evidence to suggest that within each habitat type skylarks were actively seeking out structurally or botanically different areas, or areas with greater invertebrate abundance. Certainly within set-aside this result may be expected since it is a habitat that can provide a heterogeneous structure and vegetation cover (Henderson et al., 2001; Wilson, 2001) that receives little or no pesticide application. Provisioning skylarks may well be able to access the ground, move around and detect prey with the same ease throughout this habitat so do not have to make a choice of where to forage within it. Most territories at Loddington are associated with set-aside (Boatman et al., 2000) and it was shown in Chapter 3 to be a favoured foraging area. Set-aside at Loddington is sown with many different plant mixtures (Boatman & Bence, 2000), providing a heterogeneous habitat, not just in terms of structural diversity, but also botanically. Invertebrate abundance should be high across set-aside, due to its minimal management and with it being a reservoir of many invertebrate host plant species, so the lack of evidence of skylarks selecting areas with higher invertebrate abundance over others within it is also anticipated. If skylarks are genuinely seeking out specific foraging areas within set-aside the sampling regime used to detect this may have been too coarse to identify this.

Findings of this research showed that skylarks identified accessible areas within cropped habitats. Skylarks regularly utilised crops as foraging grounds (see Chapter 3, 3.4.2.1) and were shown to forage in winter cereals with more bare ground and less crop. This result supports Buckingham (2001) who found that foraging skylarks, in winter, preferred areas with more bare ground and short vegetation that were more exposed than control sites (i.e. generally further away from field boundaries. The ease of alighting and manoeuvrability within the crop may explain this to some extent. The sward structure of winter wheat gets denser as it grows. As a result, nesting skylarks are forced to position their nests closer to tramlines, increasing their chances of predation (Donald & Vickery, 2000). In the same way, if the crop is too dense to nest in, it may be difficult for skylarks to push through and forage successfully, although I believe that birds landing in tramlines do move into the crop to forage, but maintain a distance to be able to successfully flee if necessary. Odderskaer

et al. (1997) and Schön (1999) also found that skylarks preferred to forage in areas with more bare ground even if food availability was higher elsewhere, so the fact that skylarks chose areas with more bare ground and sparse crop cover is not surprising. Invertebrate abundance itself is also likely to be affected by the microhabitat, including microclimate, availability of food, shelter and crop cover (Booij & Noorlander, 1992; Sotherton & Moreby, 1992).

In beans, provisioning skylarks foraged in areas with appreciably less bean cover than in control areas. The structure of the bean crop may explain this since legumes are fast growing and cover large proportions of the ground compared to cereal crops, limiting accessibility and movement as they grow. Beans were used as a foraging (and nesting) habitat during the start of the season only. Skylarks were therefore shown to use limited areas within the crop structure available.

The trend for less dense vegetation in foraging sites compared to control sites, within all habitat types, lends support to the hypothesis that skylarks require a vegetation structure that allows ease of movement for foraging (Odderskaer et al., 1997; Wilson, 2001), rather than areas with increased insect abundance (Odderskaer et al., 1997; Chamberlain et al., 1999a). Indeed the sward structure, in terms of height and density, may inhibit foraging use but it is also likely that foraging birds require a vegetation structure that would enable them to escape or hide from predators quickly. Birds observed pushing their way into dense beetle banks may have restricted their movement whilst seeking chick food, but beetle banks were less densely vegetated at their edges enabling birds to flit in and out whilst remaining aware of their surroundings.

Odderskaer et al. (1997) demonstrated that skylarks did not forage in crop areas with greater invertebrate abundance, but rather in places with sparse vegetation where invertebrate abundance was lower (i.e. tramlines and unsown plots). However, invertebrate samples were collected only once during his study period, one day in mid-June (the peak of the breeding season). No tests for seasonal or environmental effects could be made and, it is likely that the invertebrate community could fluctuate with time of day and local environmental conditions, across the season and between years. Another similar study, but on provisioning yellowhammers (Morris et al., 2001b), found that, in winter cereals, birds selected patches that were both rich in invertebrates and had sparser, shorter vegetation, compared to areas in which birds did not forage within the same field.

Invertebrate samples were collected across the study period (2000 - 2001), similar to this study at Loddington. Although Morris et al. (2001b) discovered that yellowhammers were more likely to return to the same areas to forage if invertebrate abundance was higher than control areas, the current study did not find any differences between skylark foraging and control areas, though it did not take into account the number of times that a provisioning adult visited that same patch. Skylarks were nonetheless frequently observed returning to the same foraging places, particularly in set-aside (as were yellowhammers).

Whilst the Loddington study never found any significant differences between vegetation structure of skylark foraging and control areas within cereals, there was a trend towards less dense vegetation at foraging sites. A preliminary study by the RSPB (Morris et al., 2003) called 'Sustainable Arable Farming for an Improved Environment' (SAFFIE) is investigating the effects of sward management in winter wheat for skylarks during the breeding season. Early results suggest that the provision of undrilled plots within winter wheat can help extend the breeding season probably by providing further nesting and feeding sites. Since cereals are the single most important habitat type for skylarks (Donald & Vickery, 2000) these plots seem to enable birds to utilise the crop to its full potential, enabling movement and detection of prey items in an otherwise dense sward structure, as suggested by Buckingham et al. (1999).

4.6.2 Skylarks and yellowhammers

Both skylark and yellowhammer are principally ground foraging farmland birds. This is the first study to simultaneously assess the microhabitat of their selected foraging places and showed that sites were similar in vegetation structure, density and botanical species composition within most habitat types. Only in set-aside was a difference seen, where skylarks foraged in areas with less oilseed rape than yellowhammers. This difference could be accounted for by their behaviour. Yellowhammers are capable of sitting on the crop and picking off insects, grain or seeds whereas skylarks always forage on the ground and therefore may require more space to move around. However, analysis could not take into account the different set-aside types, which have very different vegetation structures, due to the limited number of samples available. Therefore subtle differences in vegetation structure between skylark and yellowhammer foraging sites within the different set-aside foraging sites (e.g. kale set-aside, cereal set-aside, wildflower mixes etc) may have been

overlooked. Results from Chapter 3 showed that although set-aside is an important foraging ground for both skylark and yellowhammer they do utilise it differently. Skylarks use kale set-aside more than yellowhammers and cereal set-aside less than yellowhammers, relative to availability. Yellowhammers showed a non-significant trend for foraging in higher and denser set-aside, which may reflect the different set-aside foraging types both species selected.

In winter wheat, skylarks foraged in areas with more spiders than yellowhammers. Spiders are important constituents of both species nestling diet (Poulsen et al., 1998; Stoate et al., 1998; Wilson et al., 1999; MacCleod, 2001). This study found both species selected them more than would be expected relative to their availability (see 5.4.3.1 and 5.4.3.2). Provisioning skylarks may have taken more spiders because they were more abundant at foraging sites rather than because they were actively seeking them, or conversely they may have been actively seeking areas with higher numbers present. Yellowhammers may also have been supplementing chick diet with ripening grain (Stoate et al., 1998; Chapter 5), which may explain why they use areas with lower invertebrate abundance than do skylarks. Chapter 3 demonstrated that yellowhammers utilised cereal crops more than skylarks.

4.6.3 Song thrushes

Results from this study found little evidence to suggest that song thrushes foraged in areas that were structurally different from control sites within the same habitat type, or in areas with consistently higher invertebrate abundance. This could be due to (i) no differences between foraging and control sites or (ii) difficulties in determining different foraging and control sites, insufficient sampling techniques and possible sampling errors within their MCP foraging range. Errors associated with determining song thrush foraging habitats and where they foraged within them, are discussed in Chapter 3 (section 3.5.3.2) and Hill (1998, Appendix 4) provides a good overview of the difficulties. During field work the sampling regime was modified to fit in with what was considered practical and manageable within the realms of the PhD at the time. However, it is possible that the regime was too conservative to detect subtle differences in vegetation structure or invertebrate abundance (see sub section 4.5.4.2) and more samples should have been taken.

Problems were two-fold. Firstly, unlike with the skylark and yellowhammer projects, it was not possible to directly observe where the birds foraged, so differences in sample accuracy were not as precise as they would have been with direct observation. Secondly, determining where to collect foraging and control samples within the same habitat type was difficult due to the small MCP range sizes plotted after each breeding attempt (around 1ha), i.e. ensuring that they were taken far enough apart.

Song thrushes are known to forage on habitat boundaries such as woodland edges, hedges and ditches so it was difficult to be absolutely certain that a fix fell directly on the boundary when plotted by hand on the overlaid grid. Combining similar habitat categories for the analysis may have eliminated some of these problems. The sampling criteria set out in section 4.3.2 tried to address and eliminate potential sampling problems and ensured data were collected systematically throughout the project. However occasionally, when dealing with small habitat areas within the MCPs, it was not possible to collect control samples much greater than 10m from foraging sites, hence possibly making foraging and control samples indistinguishable in small habitat areas.

More invertebrates were present in soil cores taken in foraging than control sites in grass, woodland and boundary habitats, although this was not found to be significant. These habitats, known to be rich in earthworms (Tucker, 1992; Chamberlain et al., 1999c; Peach et al., 2004), were favoured foraging habitats (see Chapter 3, 3.4.2). When soil core data were pooled, favoured foraging habitats had higher numbers of invertebrates than cropped habitats, which were generally avoided by foraging birds (see 3.4.2.4). It is therefore possible that these results provide anecdotal evidence to support the null hypothesis that invertebrate abundance has a greater influence on provisioning song thrushes independently of habitat structure. Nevertheless, permanent pasture was used less than expected by provisioning birds, relative to availability, despite having high resources of potential nestling food. Permanent pasture was generally situated next to woodland or boundary habitats, providing accessible protective cover for foraging birds. Vegetative cover may therefore play a role in influencing foraging sites for this species on another level. As shown in Chapter 2, increased proportions of permanent pasture around the nest positively influenced nest survival rates during incubation, possibly providing the female with an important source of food whilst incubating.

Contrary to what might be expected a significantly higher worm biomass was found in samples from boundary habitats of song thrushes not provisioning young. This result could be attributable to the limited number of 'non-breeding' birds sampled using boundaries. Habitat quality within and across territories is likely to vary, perhaps accounting for this difference.

Soil penetrability is likely to affect where song thrushes forage, and it was unfortunate that the probes used in the second year of the study were not sensitive enough to examine changes throughout the season so their use was abandoned. Peach et al. (2004) found that soil hardness increased over the breeding season and worm biomass was negatively related to soil penetrability across habitats. This could result in thrushes seeking out foraging habitats that maintain a degree of wetness such as woodlands and ditches, rather than grass pastures.

4.6.4 Invertebrate sampling techniques

4.6.4.1 D-vacuum suction sampling

The D-vacuum suction sampler is commonly used for sampling ground dwelling insects, although it has been reported that the D-vacuum suction sampler under-estimates the densities of arthropod predators on arable farmland (MacLeod et al., 1995). It is a loud, heavy, vibrating machine, potentially alerting some invertebrates and providing a window of opportunity for escape. The D-vacuum sampling efficiency can vary according to vegetation height, density and environmental conditions, which can also affect invertebrate movements (Sunderland et al., 1995). Dense vegetation in some set-aside types may have been less efficiently sampled than others (e.g. second year kale set-aside compared to first year cereal set-aside or newly sown plots) and likewise in cereal crops once they are fully-grown. By taking the foraging and control samples on the same day, within the same habitat type and under the same conditions any sampling error between the samples was minimised. Samples were collected at different times of the day during the study period, depending on the time of the first watch, so should not bias towards certain insect groups activity at certain parts of the day. D-vacuum sampling could only take place in dry weather conditions, so that invertebrates did not stick to the vegetation or the net, getting damaged on removal. This occasionally hindered invertebrate collection, resulting in some missing data per nest. Further discussion of the D-vacuum sampling technique is in Chapter 5 section 5.5.2.

4.6.4.2 Soil cores

Soil cores were considered to be the best sampling technique available for measuring earthworm abundance. However, whereas the D-Vacuum sampler covers a larger area, the soil core sampled a specific, small area selected from a larger area that birds may have been foraging over. A series of soil cores may therefore have produced more meaningful invertebrate availability results for song thrushes since they forage within a space of a few metres squared within the same habitat type. The formalin extraction technique was an alternative method considered (as used by Chamberlain et al., 1999c). However, this was discarded due to the labour and time intensive nature of this technique. Since the nest was the unit of analysis and not the number of samples taken, too few samples were available from each habitat type to allow a direct comparison between foraging and control sites. To over-come this similar habitats were grouped, but despite this not all birds foraged within each habitat type, often resulting in a small sample size.

The fact that so few soil cores were taken relative to habitat area may contribute to the fact that few differences in invertebrate availability were found between foraging and control sites. Indeed this highlights the fine scale of the study, which may have been inappropriate for investigating song thrush foraging sites. A more general overview of structure and food abundance across foraging and non-foraging habitats may have been more appropriate for this species. For example, taking a fixed number of soil cores and vegetation samples across the entire breeding season in all habitat types available at Loddington and looking at differences between habitats used to forage in and those actively avoided at the end of the season. This may have identified differences in foraging patterns, eliminating difficulties in determining where birds may and may not have foraged within the same habitat type. This method would have emphasized general patterns in changing vegetation structure and invertebrate abundance across foraging and non-foraging habitat types which song thrush foraging use. To be able to carry out a sampling strategy at this level more assistance would be required or only a single species, e.g. the song thrush, should be studied.

4.6.5 Conclusions

This research provides supporting evidence that skylarks forage in areas with sparser vegetation within winter cereals but not that they forage in areas with higher invertebrate abundances (Odderskaer et al., 1997;

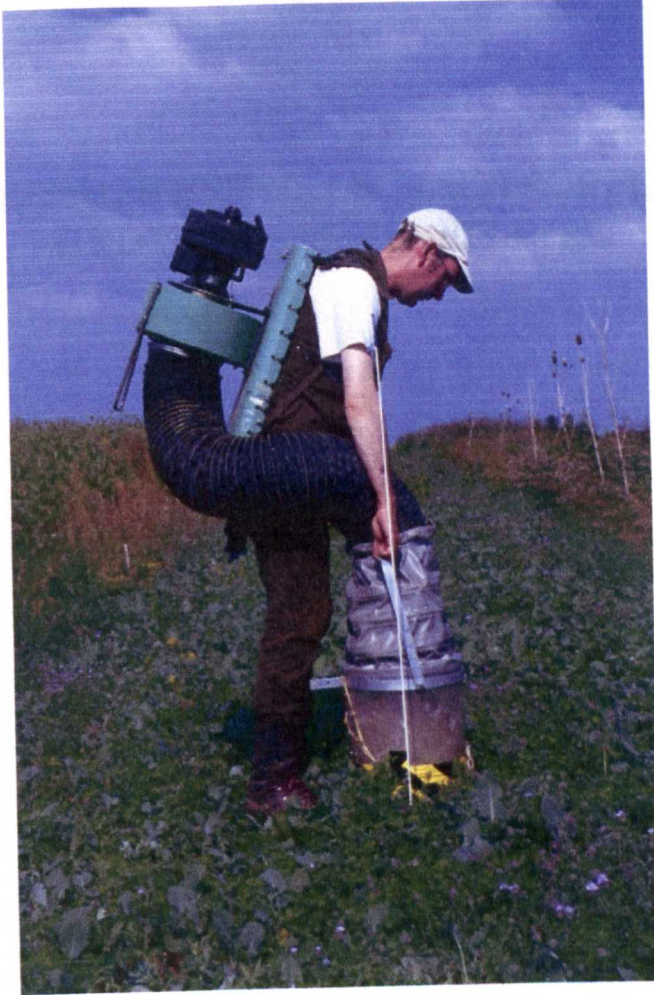
Buckingham, 2001; Morris et al., 2003). It highlights the value of the heterogeneous vegetation structure of set-aside which may enable provisioning birds to forage anywhere within this habitat, whilst emphasising that more work is needed to determine the exact requirements of foraging skylarks that will meet their feeding and nesting requirements in cereals (as Morris et al., 2003).

Skylarks and yellowhammers were found to forage in similarly structured and botanically diverse vegetation within most habitats, but skylarks foraged in areas with more bare ground in winter beans and less oilseed rape in set-aside. Skylarks foraged in areas of winter wheat with significantly more araneae than yellowhammers and with a non-significant trend towards greater total invertebrate abundance than yellowhammers. This study therefore suggests that targeted management of known foraging habitats could potentially benefit more than one passerine species that provision their young with invertebrates.

This research does not find concrete evidence to suggest that vegetation structure or invertebrate abundance influences song thrush foraging sites. However, the study was likely to have been carried out at too fine a scale to determine definitive results using radio-telemetry as a tool. On a coarser level, song thrushes were found to forage within habitat types that held higher numbers of invertebrates than cropped land, but they avoided permanent pasture (Chapter 3) despite it holding the highest biomass of potential chick food. Predation pressure, shelter and soil penetrability may affect their foraging habitat choice but this study could not examine these factors.

Since each species is a multiple nester, it is important in terms of productivity, that cropped and uncropped habitats are provided and managed to offer not just suitable nesting sites but also suitable foraging areas that allow easy access to abundant chick food prey items throughout the course of a breeding season. Organic and less intensive farming methods, alongside agri-environment schemes encouraging habitat diversity, can meet some of these requirements (Peterson, 1994; Wilson et al., 1997a; Chamberlain et al., 1999b; Aebischer et al., 2000; Chamberlain & Wilson, 2000; Freemark & Kirk, 2001).

Appendix 4, Plate 1: The D-vacuum suction sampler used to measure invertebrate abundance at foraging and control sites for skylarks and yellowhammers.



CHAPTER 5

RELATIONSHIPS BETWEEN FOOD SUPPLY, CHICK GROWTH AND CHICK DIET

5.1 Summary

1. Chick diet, growth rates and invertebrate abundance around the nests of skylarks, yellowhammers and song thrushes were investigated, with particular reference to habitat and environmental factors. Growth rates were calculated using both weight and tarsus length measurements.
2. This study showed that nestling diet of skylarks, yellowhammers and song thrushes was related to invertebrate abundance and availability at foraging sites. Invertebrates are a major component of the three species' diet, although skylark and yellowhammer nestlings were also fed unripe grain. Skylark and yellowhammer nestlings were fed insect larvae and araneae more than would be expected relative to their availability. Earthworms and molluscs were the main components of song thrush nestling diet.
3. Chick diet did not change with age for any of the study species. Adults were generally consistent in what they fed their chicks over the breeding season and between years, although a wide range of invertebrate prey items was fed to chicks.
4. For skylarks, growth rates were positively associated with the proportion of managed set-aside around the nest and negatively associated with the proportion of 'other' habitats. The proportion of permanent pasture around the nest was weakly and positively correlated with song thrush growth rates, but not significantly so. No other habitat effects were detected on any of the study species with regard to chick growth rates.
5. No environmental factors significantly influenced growth rates of skylark and song thrush chicks. Temperature had a significant negative effect on yellowhammer chick tarsus growth rates, but only when including data from all nests (i.e. without excluding those that experienced partial brood loss).
6. Invertebrate abundance around the nests did not have any effect on chick growth rates for any of the three species. However at a finer scale, the proportion of araneae in skylark chick diet was shown to have a significant negative influence on nestling growth rates. No other dietary component was shown to affect the growth rates of yellowhammer and song thrush nestlings.
7. There was weak non-significant evidence of a decline in chick growth rates of song thrush nestlings when predator control was not taking place. However, predator control ceased for only one year of the study.

8. Habitat management practices which serve to increase invertebrate abundance, diversity and accessibility will help to improve diet and chick growth rates, perhaps contributing to increased fledging rates of some species.

5.2 Introduction

Food-supplies during the breeding season may influence the survival of adult birds or their nestlings (Newton, 1998), which in turn could affect breeding bird densities. For the nationally declining skylark, yellowhammer and song thrush, which all feed their young a mainly invertebrate diet, the availability and abundance of certain invertebrate groups may affect their nestling growth and possibly survival. This chapter concentrates on their chick diet and invertebrate availability and abundance to provisioning adults.

On arable farmland one of the greatest risks to invertebrate abundance is the use of pesticides, insecticides and herbicides. These can affect nestling survival, mainly indirectly, by killing invertebrates or invertebrate host food plants, which are also a supply of seeds and leafy food to birds (Campbell et al., 1997; Moreby & Southway, 1999). As pesticide application increased over the decades, this coincided with a decrease in many chick food invertebrate groups (Campbell et al., 1997). In their review of the diet of 26 granivorous bird species of European temperate farmland (including skylark and yellowhammer), and the effects of agricultural practices on their invertebrate and plant foods, Wilson et al. (1999) include the invertebrate groups orthoptera, hymenoptera, arachnida, coleoptera, hemiptera and diptera (mainly Tipulidae and their larvae) as the main important chick food sources. Many of these invertebrate groups are sensitive to pesticide application (Sotherton, 1991; Wilson et al., 1999) and have decreased alongside agricultural intensification (Aebischer, 1991; Campbell et al., 1997).

Pesticide use has greatly increased on farmland since the late 1950s, mirroring declines of many invertebrate and plant species (see Sotherton & Self, 2000 for a review). Ewald & Aebischer (2000) recorded a general increase in pesticide use over the 26 - year study period in the South Downs, West Sussex. They reported that between 1970 and 1995 the number of weed taxa susceptible to herbicides applied increased from 22 to 38,

thereby reducing many more invertebrate host plants over this period. Aebischer & Potts (1990) report that the total number of invertebrates on the same study site in Sussex, comprising over 100 fields, has decreased by one quarter between 1970 and 1989 and detail a widespread decline in araneae and opiliones, lepidoptera, aphididae, hymenoptera and all coleoptera, all of which are important chick food items. Earthworms and their abundance are also affected by cultivations (ploughing), cropping patterns (availability of organic food), fertilisation (organic and inorganic) and crop protection (pesticide use) (Edwards & Bohlen, 1996). Carbamate fungicides and the molluscicide methiocarb are known to have toxic effects on non-target invertebrates such as earthworms (Edwards, 1984), as well as snails and slugs (Campbell et al., 1997), which are the other major component of both adult and nestling song thrush diet.

The grey partridge (*Perdix perdix*) is the best-known example of a farmland bird where the indirect effect of pesticides has been shown to be a significant factor contributing to the population decline (Poulsen & Aebischer, 1995; Campbell et al., 1997; Potts, 1997). The survival of chicks up to 3 - weeks old was directly related to invertebrate availability in cereal fields. Herbicides removed the host plants of many chick-food invertebrate species making them less available and harder to find, leading to starvation of chicks and a reduction in chick survival rates. If food availability is reduced, it is likely that nestlings could suffer poor growth rates and body condition as a consequence. The decline in invertebrate supply through pesticide use has been implicated in the decline of skylarks in Switzerland (Jenny, 1990b), ciril buntings (Evans et al., 1997) and corn buntings (Brickle et al., 2000), whose nestling diet is comparable to that of grey partridge chicks, yellowhammers (Morris, 2002) and many other passerine species (Campbell et al., 1997).

Understanding nestling diet, in relation to what is available to the study species, is of primary concern when trying to determine which dietary components are most important and how these invertebrate groups can be enhanced through habitat management. Dietary preferences may indicate that certain invertebrate groups are preferred above others, despite possibly being of lower nutritional value. Researchers should be open to subtle variations in both quality and quantity of potential invertebrate foods across a breeding season, as demonstrated by Naef-Daenzer et al. (2000). Naef-Daenzer et al. (2000) found that Great tits (*Parus major*) fed nestlings mainly spiders until caterpillars reached a certain size, not when caterpillars increased in abundance, and that nestling growth rate was then significantly influenced by the weight of caterpillars.

Management techniques should therefore aim to increase and maintain the diversity of a large number of important chick food invertebrate groups like those suggested in Campbell et al. (1997), Thomas & Marshall (1999) and Wilson et al. (1999) at any one time.

Chick growth and development, particularly in altricial species, is likely to be determined by the composition of the diet fed to them (e.g. Johnson, 1993; Naef-Daenzer et al., 2000), the number of feeding visits that parents make to the nest (e.g. Naef-Daenzer & Keller, 1999) and the effort the parents make to get that food (O'Connor, 1984). If invertebrate availability is reduced, provisioning adults may have to travel further to find high quality feeding grounds, carry more prey items back to the nest, or make increased trips to the nest, all of which may be at a cost to their own survival in order to fledge their young. In multi-brooded species, such as the study species, this could have a detrimental affect on the number of breeding attempts pairs can make per year, as well as on adult mortality.

Adult skylark, yellowhammer and song thrush feed their chicks largely a diet of invertebrates. Adult skylark and yellowhammer diet is however predominately granivorous with leafy matter, particularly in the autumn, winter and spring months (Green, 1978, 1980; Campbell et al., 1997; Stoate & Szczur, 1997; Donald et al., 2001a). Adult song thrush diet remains similar to that of nestlings, with earthworms forming a large constituent of their diet (Gruar et al., 2003). Skylark and yellowhammer chick diet changes over time, as more and more of their diet is made up of grain with age. When this transition fully takes place is not known; although it is likely that it occurs post-fledging and once independence has been reached. One may not expect song thrush diet to change with age since nestling and adult diet compositions are similar, although there may be seasonal changes due to differences in invertebrate availability or abundance over the year.

Two potential factors affecting chick diet composition were investigated in this study, (i) chick age and (ii) invertebrate abundance. Previous studies showed no change in diet with age for yellowhammers (Stoate et al., 1998) whilst Poulsen et al. (1998), Weibel (1999) and Donald et al. (2001d) demonstrated changes in skylark chick diet with age. To date, no documented study has examined song thrush chick diet in relation to age, although a recent study by the RSPB on the diet of song thrush chicks, fledglings and adult birds (Gruar et al., 2003) revealed that chick diet comprised more insect larvae than the diet of fledglings or adult birds did. The

foraging strategy of a few intensively studied provisioning farmland bird species has been found to be largely selective, in terms of selecting certain prey items to feed their chicks (Evans et al., 1997; Poulsen et al., 1998; Stoate et al., 1998; Brickle & Harper, 1999; MacCleod, 2001; Donald et al., 2001d), although some species could be choosing prey at random from what is available. The hypothesis being tested in the current study was therefore “Provisioning birds show clear selection for some invertebrate taxa over others relative to their availability”. Management techniques used at Loddington to increase invertebrate abundance and availability include the creation of conservation headlands, which restrict pesticide use around crop edges to encourage weeds thus supporting invertebrates, field margins and other herbaceous vegetation, which receive no pesticide application, and the management of hedgerows and woodland (Stoate and Szczur, 2001b). Many techniques were developed and implemented at Loddington and have been demonstrated to benefit much wildlife (Boatman et al., 1999; Boatman et al., 2000).

This study also investigates the relationship of diet on nestling growth rates. Growth measurements were taken from chicks in order to investigate the effects of several measured environmental and non-environmental variables, which could influence chick growth and survival. Food availability can affect chick weight (Brickle, 1999; MacCleod, 2001) and weight at fledging could affect future survival in some species (Magrath, 1991; Naef-Daenzer et al., 2001; Perrins & McCleery, 2001).

Although the exact causes of many farmland bird declines are still poorly understood despite growing research, many studies acknowledge that factors affecting food availability and abundance are important, which in turn will affect diet composition. Species-specific diet studies are therefore important to determine which invertebrates are selected for from those available. This chapter does not take into account predation pressures per se or the effect of pesticide application on invertebrates in available habitats, although it is recognised these factors may contribute to declines in growth rates, chick condition and survival of some bird species (Morris, 2002; Boatman et al., 2004).

The aims of this chapter are therefore to investigate i) diet of skylark, yellowhammer and song thrush nestlings at Loddington, ii) whether nestling diet changes with age and invertebrate abundance and iii) whether diet and environmental factors can affect nestling growth rates.

5.3 Methodology

5.3.1 Collection of data

Nests were located and monitored as described in Chapter 2 section 2.3.1. Data were available in 2000, 2001 and 2002 for skylark and song thrush and in 2000 only for yellowhammer.

5.3.1.1 Invertebrate abundance and availability

Invertebrate abundance samples were collected at identified foraging sites with a D-vacuum suction sampler or a soil corer according to methods described in Chapter 4 section 4.3.1.4 and 4.3.2. Invertebrate samples were collected after the first foraging observation period unless rain prevented it. D-vacuum sampling is a recognised method for sampling ground dwelling insects (Austen, 1996), many of which are prey items for skylarks and yellowhammers. A soil corer is useful for sampling the major song thrush prey items.

Analyses based on invertebrate samples from D-vacuum suction samples assumed that invertebrates collected were representative of those available to birds at their foraging sites in each habitat type.

5.3.1.2 Nestling diet

5.3.1.2.1 Skylark, yellowhammer and song thrush neck ligatures

A licence to use neck ligatures was granted from English Nature. These were used to determine what provisioning adults were feeding their chicks. Generally they were put on each chick in a brood immediately after each foraging watch ended (see Chapter 3, section 3.3.1.1), although neck ligatures were also put on chicks when there was no time to carry out a foraging watch. This method of measuring diet is more invasive than collecting and analysing faecal samples, but has the advantage that food items are usually intact when collected which subsequently facilitates identification to a higher level than is otherwise possible. Measuring diet using neck ligatures may bias against small invertebrates that could pass down the throat and remain

undetected, while faecal sampling may bias against soft-bodied invertebrates with little keratin that would be undetectable in the faecal sample (Moreby & Stoate, 2000). Poulsen & Aebischer (1995) found no detectable difference in diet composition between faecal and neck ligature samples from nestling skylarks and Moreby & Stoate (2000) detected no differences in invertebrate groups or diversity between the two sampling methods for nestling yellowhammers. Since time was limited in this study it was therefore deemed acceptable to work with neck ligature samples to investigate chick diet for skylark and yellowhammer.

Neck ligatures were made from flesh coloured silk embroidery thread. After each foraging watch, chicks were placed in a cotton bag and taken approximately 5 metres from the nest. Pre-prepared neck ligatures were tied securely around the base of the neck of each chick in a brood, cutting the ends close to the non-slip knot at the base of the neck. Ligatures were tied tight enough to allow chicks to breathe and beg easily but not to allow food items to pass through to the stomach. After replacing the chicks in the nest and leaving the area for 45 - 50 minutes the nest was re-approached and the chicks again collected in a bag and taken away from the nest. The gape and throat of each chick was checked and any prey items removed with fine-pointed tweezers and stored in a tube with 80% industrial methylated spirits (IMS), with date, chick identification, nest code and age labelled on it. The neck ligatures were cut off with fine-pointed scissors and chicks were replaced in the bag and returned to the nest. Invertebrate throat samples were identified at the end of each season to family or order level.

5.3.1.2.2 Song thrush faecal samples

Neck ligature samples from song thrush chicks were generally not as productive as those for skylark and yellowhammer. Therefore in order to maximise the opportunity of examining song thrush nestling diet faecal samples were also collected from nestlings if they defaecated when being handled. Samples were kept in glass sample tubes filled with 80% IMS with a label recording date, chick age, nest code and individual chick marking. If exact chick age was not known, an estimate was made using experience from other brood development and a growth chart made in the first year of the study. Unfortunately, unlike skylark and yellowhammer chicks, song thrush chicks did not defaecate each time they were handled. Faecal samples from the other two species were also collected but time constraints prevented them from being analysed.

Faecal sacs were broken up and gently sieved using a 210 μ m sieve. Their separated contents were identified to family or order level under a binocular microscope using methods described by Moreby (1988). Body parts were counted in order to estimate the minimum number of individuals of each group in a faecal sac, so the minimum number of individuals present was recorded. For example, if the faecal sample contained 2 beetle legs one individual was recorded, if a sample contained 2 carabid heads then 2 beetles were recorded and so on. Samples with snail fragments were recorded as one individual, one snail whorl – 1 snail, 1 radula – 1 snail. If a sample recorded shell remains, 2 radulae and 1 internal whorl then 2 individuals were recorded.

Earthworm setae numbers ranged widely between faecal samples (0-279, n = 72). Green & Tyler (1989) found that an average of 267 setae per worm passed through adult captive stone curlew (*Burhinus oedicemus*) in their study of stone curlew diet. Therefore numbers of earthworms were counted as one if a sample contained 267 setae or less and 2 if more. This approach assumes that similar proportions of setae pass through the digestive systems of nestling song thrush and adult stone curlew but the analysis takes into account relative proportions of prey items, not exact amounts.

5.3.1.3 Chick growth

Chicks were individually marked with coloured felt-tip pens on their tarsus, head or wings. Each chick in a brood was weighed between hatching (day 0) and up to day 7 for skylarks, day 8 for yellowhammers and 10 for song thrush using an electronic balance to an accuracy of 0.1g. The tarsus length of each chick was also measured using dial callipers to the nearest 0.1mm, from the depression of the inter-tarsal joint to the end of the bent foot. If chicks were being measured after a watch, to minimise time spent at the nest, they were weighed and measured after throat samples had been collected. Brood means at each age were used in subsequent analyses since the measurements from individual chicks in a brood were not independent.

5.3.1.4 Other variables investigated

Foraging distance

Foraging distance was taken as the straight-line distance from the nest to the place where the bird was seen foraging (for details see Chapter 3, section 3.3.1.1). The mean foraging distance from all foraging visits per nest was calculated and used in the analysis.

Habitat proportions surrounding nests

Habitat proportions surrounding each nest used in the analysis were calculated using methods described in Chapter 3 section 3.3.2 and 3.3.4 to see whether habitat influenced growth. A common radius of 118m was set around each skylark and song thrush nest and 191m around each yellowhammer nest.

Weather variables

Variables that were significantly important to nest survival for each species were calculated using methods described in Chapter 2, section 2.3.4. They were included in the analysis of chick growth.

5.3.2 Data analysis

Analyses are based on data collected in 2000, 2001 and 2002 for skylark and song thrush and 2000 for yellowhammers. Invertebrate data were $\ln(x+1)$ transformed, worm abundance was square root transformed and foraging distance was $\ln(x)$ transformed to normalise the distributions. Where more than one year of data was used a year factor was entered into the analysis to test for a year effect before continuing.

5.3.2.1 Changes in chick diet with age

This analysis aimed to detect whether adult birds fed their young different invertebrate groups at different ages. For each species, data from neck ligature or faecal samples collected at each age (days) per brood were pooled and averaged, because samples from the same brood were not considered independent. Data were then further pooled into two age groups for each species and a mean proportion per nest calculated (Table 1). The two age groups were dictated by sample size. All nests with data from neck ligature samples were included in

the analysis and each nest was treated as an independent sample. For song thrush, faecal samples were also included in the analysis.

Table 1: Age groups for neck ligature and faecal sample analysis

Species	Age group 1 (days)	Age group 2 (days)
<i>Skylark</i>	Neck ligature - 3 - 4	Neck ligature - 5 - 7
<i>Yellowhammer</i>	Neck ligature - 2 - 5	Neck ligature - 6 - 8
<i>Song thrush</i>	Neck ligature - 3 - 5	Throat - 6 - 8
	Faecal - 1 - 5	Faecal - 6 - 10

Different invertebrate groups were pooled for analysis according to the percentages present across broods (Table 2), by combining either similar taxa, life cycle stages or where very low percentages occurred in the diet, (Table 5, 6, 7, 8).

Analyses were conducted in Systat vs 10. Univariate tests were performed using ANOVA to determine if there were any differences in chick diet with age. MANOVA could have been used to test for effects on all invertebrate groups simultaneously, as was tried, but the multivariate models would not converge due to the nature of the data, hence the valid univariate approach was adopted. The dependent variables were the separate insect groups, and the factors tested included year, age group and month. Data were weighted by the number of successful neck ligature samples obtained per brood per age group, to account for the different number of successful samples gathered per brood. The same brood could appear in both age groups (41% of skylark broods, 33% of yellowhammer broods and 17% and 16% of song thrush in neck ligature and faecal analysis), but for the purposes of this analysis they were assumed to be independent. A sequential Bonferroni correction factor was applied to any significant result (Rice, 1989), as the process made multiple comparisons across invertebrate groups.

Table 2: Invertebrates groups used for analysis.

Bird species	Invertebrate group	Contents
<i>Skylark and yellowhammer</i>	Araneae	Wolf spiders, non-wolf spiders, opiliones and egg sacs
	Lepidoptera (adults)	
	Coleoptera (adults)	Mainly carabidae but also staphylinidae
	Insect larvae	Including tipulidae, symphatica, lepidoptera, carabidae and other beetle larvae, other pupae
	Diptera (adults)	Mainly tipulidae and empidae
	Other insects	Orthoptera/dermaptera, neuroptera, homoptera, isopoda/gastropoda, chilopoda/diplopoda, aphidae and parasitica
<i>Song thrush</i>	Gastropoda	Slugs and snails
	Earthworms	
	Insect larvae	Including beetle larvae, diptera larvae and others
	Coleoptera (adults)	
	Flying insects	Diptera and hymenoptera
	Others	Collembola, dermaptera, homoptera and parasitic wasps
	Araneae	For faecal analysis groups only

5.3.2.2 Invertebrate availability and chick diet

The effect of invertebrate availability on provisioning skylark and yellowhammer choice of chick food prey items was analysed using compositional analysis (see Chapter 1, Appendix 1). Analysis of invertebrate composition was based on the proportion of invertebrates in each taxonomic group in a sample. Data were unit-sum constrained since the proportions from any nest summed to one. The relative proportions of invertebrates collected from throat samples constituted the ‘used’ part of the analysis and the relative proportions of invertebrates collected in D-vacuum samples for that particular nest constituted the ‘available’ part of the data set. This analysis assumes that throat sample composition approximates to actual diet

composition and that D-vacuum invertebrate samples approximate to the invertebrate availability to foraging skylarks and yellowhammers around their nests.

Data from nests involved in foraging watches, together with the collection of both successful neck ligature samples and D-vacuum invertebrate samples from foraging sites, were used in the analysis. The number of invertebrate groups was kept to a maximum of 6 for both skylark and yellowhammer, to increase the power of the test.

Groups investigated were:

1. Araneae,
2. Coleoptera adults,
3. Insect larvae (including tipulidae, symphyta, lepidoptera, carabidae and other beetle larvae, other pupae),
4. Diptera adults,
5. Parasitica
6. 'Other insects' (Orthoptera/dermaptera, neuroptera adults, homoptera, hemiptera, isopoda/gastropoda, chilopoda/diplopoda, aphidae and parasitica) + Lepidoptera adults.

These invertebrate groups were chosen for the following reasons. Lepidoptera adults were occasionally fed to chicks but were rarely found in D-vacuum samples, so were combined with the 'other insect' group to avoid large numbers of missing values in the 'available' columns. Collembola were excluded from the 'Other insects' group because, although they were often numerous in numbers in the D-vacuum samples, they were never found in the throat samples and may have biased the results (despite being listed in Wilson et al., 1997b). Parasitica formed their own group for this analysis since they were abundant in the D-vacuum samples and therefore available and abundant as possible chick food items.

Song thrush data from neck ligatures or faecal samples and soil cores were not analysed in this way. Analyses of faecal samples revealed that song thrushes take a varied amount of prey items, consistent with Gruar et al. (2003). However, only 4 sets of comparative data with soil core and song thrush faecal samples were available so composition analysis could not be carried out.

5.3.2.3 Chick growth rates

This analysis investigates various factors and variables, (Table 3), which could affect chick growth rate using data from two or more sets of mean brood biometric measurements. Data were available for many nests at several (known) different ages (days). Nests were included in the analysis only if the number of chicks measured on each visit was the same as the number of eggs that hatched to avoid any bias caused by the effects of brood reduction. Two types of analysis were carried out:

1. Using the difference between the first two sets of brood mean measurements divided by the number of days between measurements (called *GR 1* or *Tarsus 1*) giving the grams of weight gained per day or the mm of tarsus length gained per day. This analysis investigated a short time period in chick growth and was therefore more sensitive to short-term environmental or behavioural changes (e.g. a day of heavy rain, a day of extreme heat, provisioning bird being chased by a predator).
2. Using the difference between the first and last brood mean measurements taken divided by the span of measurement days giving the grams of weight gained per day or the mm of tarsus length gained per day (called *GR total* or *Tarsus total*). This analysis investigates changes in chick growth rates over a longer period of time and is therefore less sensitive to short-term environmental changes and more likely to detect factors or variables that might genuinely affect chick growth rates.

For each analysis, the mean age group was calculated so that age could be included in the modelling process. For example, a brood measured on day 3 and subsequently on day 8 was given the average age of 5.5. Only one estimate of growth rate per brood was therefore included in the analysis. Variables that significantly affected nest survival analysis (Chapter 2, section 2.5.5) and the proportion of diet composition per nest for each species were also included in the analysis.

Analysis was carried out in Genstat vs 6, using a general linear forward-step modelling procedure. The response variate was growth rate (either weight or tarsus length tested separately for *GR total* and *Tarsus total* and *GR 1* and *Tarsus 1*) using normal errors and an identity link function. The variables entered into the model for each species are described in Table 3. Each variable was fitted in turn to the model to investigate its

influence on chick growth rate per day (either weight or tarsus length). Sample sizes varied in the univariate models since not all variables were available for each nest. Once all the univariate variables that significantly explained variation in growth rates alone had been identified, a minimum adequate (multivariate) model was built by adding the significant variables into the model in order of their significance and retaining them if they maintained their significance. Non-linear relationships were also examined by including a quadratic function of the predictor variable (e.g. clutch size) in the forward-selection procedure. Residuals were inspected to check for normal errors.

5.4 Results

5.4.1 General results

5.4.1.1 Using neck ligatures to investigate chick diet

Neck ligature samples were collected from a total of 43 skylark, 20 yellowhammer and 21 song thrush nests over the periods in which they were studied. The mean abundance and mean proportional abundance of diet composition and the overall percentage occurrence of each group for each species (including grain) are summarised in Tables 4, 5 and 6. Non-invertebrate material was included in Tables 4 and 5, although not incorporated in the subsequent analysis, to show that it formed an important part of nestling diet since it was fed to 29% of skylark broods and of 75% yellowhammer broods.

Prey items fed to chicks had often been manipulated in some way. For example, parent birds regularly removed the elytra of large carabid beetles before feeding them to chicks and worms were broken up into segments, making the prey easier for the adults to handle and the chicks to swallow safely. Insects from neck ligature samples were found to be whole enough to easily aid identification through a microscope.

Table 3: Factors and variables tested to investigate their effects on chick growth rate and tarsus length in skylark, yellowhammer and song thrush chicks. Proportion of habitats around the nests is taken from 118m radii of skylark and song thrush nests and a 191m radius around yellowhammer nests. * = Included in this species analysis, - = variable not tested for in this species.

Variable to be tested	Type of variable	Skylark	Yellowhammer	Song thrush
<i>Growth rate (g per day)</i>	Response variate	*	*	*
<i>Mean age</i>	Continuous	*	*	*
<i>Year (2000, 2001, 2002)</i>	Factor	*	-	*
<i>Clutch size</i>	Factor	*	*	*
<i>Brood size</i>	Factor	*	*	*
<i>Outcome (success or fail)</i>	Factor	*	*	*
<i>Invertebrate abundance $\ln(x+1)$</i>	Continuous	*	*	*
<i>Mean foraging distance from nest</i>	Continuous	*	*	-
<i>Proportion of habitat areas around the nest site (from Chapter 3)</i>	Continuous	*	*	*
<i>Arcsine transformed cover density at nest</i>	Continuous	*	-	-
<i>Log rainfall 5 days prior to hatch date</i>	Continuous	*	*	*
<i>Inc mean (Log mean temperature over a 5 day period before hatch date)</i>	Continuous	*	*	*
<i>Month</i>	Factor	*	*	*
<i>Predator control (1 or 2)</i>	Factor	*	-	*
<i>Farm centre or border (1 or 2)</i>	Factor	*	-	*
<i>Habitat type the nest was in</i>	Factor	*	-	*
<i>Date of last egg (start if incubation)</i>	Continuous	*	-	*
<i>Month young in nest</i>	Factor	*	-	*
<i>Young mean (mean temperature over a 5 day period prior to hatching)</i>	Continuous	*	*	*
<i>Diet composition</i>	Continuous	*	*	*
<i>Cover density at the nest</i>	Continuous	*	-	-

5.4.1.2.1 Skylark chick diet

Approximately 31% of skylark chick invertebrate diet (measured in numbers not biomass) was made up of insect larvae, which were fed to 75% of all broods (Table 4). The next most important groups were adult coleoptera, forming 18% of all neck ligature samples, of which at least 64% of all broods were fed carabids, and araneae, constituting 14% of all samples and fed to 71% of all broods. Although 'other insects' made up around one fifth of all samples this group was formed by combining all 'minor' invertebrate families contributing less than 4% to all samples.

Diptera adults formed less than one tenth of all samples (9.3%) but were present in 41% of brood neck ligature samples. Diptera in samples comprised mainly adult tipulidae and empidae rather than the smaller nematocera or other larger diptera.

Table 4: Composition of skylark neck ligature samples ($n = 57$) per nest ($n=31$) during the study period 2000-2002. The table includes the mean number of grains and the mean number of each invertebrate taxon per brood, \pm SE, the frequency of occurrence of each food item group (%) in all broods combined and the mean proportion of invertebrate groups comprising nestling diet (2000 = 10 broods, 2001 = 12 broods and 2002 = 9 broods).

Invertebrate group	All years $n = 31$				2000 $n = 10$			2001 $n = 12$			2002 $n = 9$		
	Mean	SE	%	Prop	Mean	SE	%	Mean	SE	%	Mean	SE	%
Grain	0.741	0.254	29.03		1.300	0.578	50.00	0.583	0.358	25.00	0.333	0.333	11.11
Seeds	0.129	0.090	6.45		0.000	0.000	0.00	0.167	0.167	8.33	0.222	0.222	11.11
Araneae	2.032	0.611	70.97	0.143	1.500	0.543	70.00	1.000	0.348	58.33	4.000	1.878	88.89
Homoptera	0.548	0.249	25.81	0.039	1.100	0.674	50.00	0.250	0.179	16.67	0.333	0.333	11.11
Heteroptera	0.129	0.061	12.90	0.009	0.300	0.153	30.00	0.083	0.083	8.33	0.000	0.000	0.00
Lepidoptera adults	0.468	0.165	29.03	0.033	0.400	0.221	30.00	0.333	0.188	25.00	0.722	0.465	33.33
Carabids	1.790	0.379	64.52	0.126	1.700	0.616	70.00	1.167	0.458	50.00	2.722	0.909	77.78
Other beetles	0.968	0.336	35.48	0.068	0.800	0.442	30.00	1.000	0.492	41.67	1.111	0.873	33.33
Insect larvae/pupae	4.419	0.959	75.19	0.311	3.300	1.350	60.00	7.083	1.936	100	2.111	0.841	55.56
Diptera adults	1.323	0.381	41.94	0.093	1.300	0.651	40.00	1.417	0.783	33.33	1.222	0.465	55.56
Others	0.581	0.216	32.26	0.041	1.000	0.596	40.00	0.500	0.230	33.33	0.222	0.147	22.22
Orthoptera	0.065	0.045	6.45	0.005	0.000	0.000	0.00	0.167	0.112	16.67	0.000	0.000	0.00
Dermaptera	0.097	0.072	6.45	0.007	0.000	0.000	0.00	0.083	0.083	8.33	0.222	0.222	11.11
Neuroptera	0.161	0.161	3.22	0.011	0.000	0.000	0.00	0.417	0.417	16.67	0.000	0.000	0.00
Aphids	1.612	1.365	9.68	0.114	0.100	0.100	10.00	4.083	3.496	16.67	0.000	0.000	0.00

5.4.1.2.2 Yellowhammer chick diet

Insect larvae were also the main invertebrate component of yellowhammer neck ligature samples (number not biomass), comprising 46% of invertebrate diet, and being fed to 55% of all broods (Table 5). The next most important invertebrate group was diptera adults, making up 18% of diet, and being fed to 45% of all broods. coleoptera comprised 12% of yellowhammer samples, being fed to at least 40% of all broods, and araneae constituted only 6% of all samples even though they were fed to 35% of all broods. Grain was a more important constituent of diet, being fed to 75% of all broods and forming around one fifth of all samples, compared to skylarks where grain was present in the diet of 29% of all broods.

Table 5: Composition of yellowhammer neck ligature samples (n = 42) per brood (n=20) during 2000 breeding season. The table includes the mean number of grains and mean number of each invertebrate taxon per brood, \pm SE, the frequency of occurrence of each food item group (%) per month (brood samples combined) and the proportion of the invertebrate abundance in overall nestling diet.

Group	All months n = 20				June n = 7			July n = 7			August n = 6		
	Mean	SE	%	Prop	Mean	SE	%	Mean	SE	%	Mean	SE	%
<i>Grain</i>	2.500	0.484	75.00		2.143	1.079	42.86	3.000	0.756	100	2.333	0.667	83.33
<i>Araneae</i>	0.650	0.254	35.00	0.064	0.571	0.571	14.29	0.857	0.459	42.86	0.500	0.224	50.00
<i>Aphids</i>	0.050	0.050	5.00	0.005	0.143	0.143	14.29	0.000	0.000	0.00	0.000	0.000	0.00
<i>Other</i>	0.150	0.109	10.00	0.015	0.143	0.143	14.29	0.000	0.000	0.00	0.333	0.333	16.67
<i>arthropods</i>													
<i>Hompotera</i>	0.400	0.275	10.00	0.039	0.000	0.000	0.00	0.000	0.000	0.00	1.333	0.843	33.33
<i>Lepidoptera</i>	0.350	0.131	30.00	0.034	0.429	0.297	28.57	0.429	0.202	42.86	0.167	0.167	16.67
<i>adults</i>													
<i>Carabids</i>	0.850	0.406	40.00	0.083	2.143	1.010	85.71	0.143	0.143	14.29	0.167	0.167	16.67
<i>Insect</i>	4.650	1.664	55.00		8.143	4.251	57.14	3.429	1.343	71.43	2.000	1.633	33.33
<i>larvae/pupae</i>				0.456									
<i>Other</i>	0.400	0.275	10.00	0.039	1.143	0.738	28.57	0.000	0.000	0.00	0.000	0.000	0.00
<i>beetles</i>													
<i>Diptera ads</i>	1.850	0.737	45.00	0.181	2.143	1.696	28.57	2.571	1.288	57.14	0.667	0.333	16.67
<i>Others</i>	0.850	0.425	30.00	0.083	1.286	1.128	28.57	0.429	0.297	28.57	0.833	0.543	33.33

5.4.1.2.3 Song thrush chick diet

Song thrush throat samples revealed that earthworms were present in the diet of 72% of broods, forming 35% of samples, followed by gastropods found in 44% of broods and forming 26% of the diet (Table 6). Flying insects were found in 11.11% of all samples, (but only from 2 broods), forming 26% of the diet. Only one sample was recorded with non-invertebrate material – two cherry stones in one chick's gape (not included in Table 6).

5.4.1.2 Using faecal samples to investigate song thrush chick diet

73 song thrush chick faecal sacs were analysed from 44 broods. Table 7 shows the mean composition (i.e. the average number of individuals in each group per brood) of invertebrates in the diet estimated through this analysis.

Faecal sample composition was similar to the throat samples. The major components of song thrush chick diet in faecal samples were earthworms, present in 98% of all samples forming 27% of the diet and gastropoda, present in 77% of brood samples also forming 27% of all samples. Araneae and coleoptera were present in 43% and 47% of all brood samples respectively, making up 10% and 13% of faecal samples. Flying insects were present in 40% of all samples making up 11% of the diet.

Table 6: Composition of song thrush neck ligature samples (n = 31) from 18 broods during the study period 2000-2002. The table includes the mean number of each invertebrate taxon per brood, \pm SE, the frequency of occurrence of each food item group (%) in all broods and the mean proportions per brood (2000 = 8 broods, 2001 = 4 broods and 2002 = 6 broods).

Invertebrate group	All years n = 18			2000 n = 8			2001 n = 4			2002 n = 6		
	Mean	SE	%	Prop	Mean	SE	%	Mean	SE	%	Mean	SE
<i>Gastropoda</i>	1.056	0.508	44.44	0.275	1.500	1.086	50.00	0.250	0.250	25.00	1.000	0.516
<i>Earthworm</i>	1.333	0.379	72.22	0.348	1.125	0.227	87.5	2.500	1.500	100.00	0.833	0.477
<i>Coleoptera adults</i>	0.222	0.222	5.56	0.058	0.500	0.500	12.5	0.000	0.000	0.00	0.000	0.000
<i>Insect larvae</i>	0.167	0.121	11.11	0.043	0.250	0.250	12.5	0.000	0.000	0.00	0.167	0.167
<i>Flying insects</i>	1.000	0.758	11.11	0.261	1.625	1.625	12.5	0.000	0.000	0.00	0.833	0.833
<i>Araneae</i>	0.056	0.056	5.56	0.014	0.000	0.000	0.00	0.000	0.000	0.00	0.167	0.167

Table 7: Composition of song thrush faecal samples (n = 73) from 44 broods during the study period 2000-2002. The table includes the mean number of each invertebrate taxon per brood, \pm SE, the frequency of occurrence of each food item group (%) in all broods and the mean proportion per brood of each invertebrate group comprising nestling diet (2000 = 9 broods, 2001 = 22 broods and 2002 = 44 broods).

Invertebrate group	All years n = 44			2000 n = 9			2001 n = 22			2002 n = 13		
	Mean	SE	%	Prop	Mean	SE	%	Mean	SE	%	Mean	SE
<i>Earthworm</i>	1.591	0.154	97.72	0.267	2.222	0.596	88.89	1.409	0.142	100.00	1.462	0.183
<i>Spider</i>	0.591	0.123	43.18	0.099	1.222	0.401	66.67	0.409	0.126	36.36	0.462	0.183
<i>Beetle</i>	0.750	0.156	47.27	0.126	0.667	0.236	55.56	0.727	0.248	36.36	0.846	0.296
<i>Insect larvae</i>	0.227	0.091	15.15	0.038	0.556	0.338	33.33	0.045	0.045	4.55	0.308	0.175
<i>Fly</i>	0.659	0.152	40.15	0.111	1.000	0.408	77.78	0.591	0.225	31.82	0.538	0.215
<i>Others</i>	0.500	0.140	34.15	0.084	0.667	0.289	44.44	0.409	0.234	22.27	0.538	0.183
<i>Gastropoda</i>	1.636	0.307	77.27	0.275	2.556	1.107	88.89	1.682	0.369	81.82	0.923	0.288

5.4.2 Changes in chick diet with age

5.4.2.1 Skylarks

A total of 29 skylark nests and 43 samples were included in the analysis. After a sequential Bonferroni correction was applied, there were significant differences in the abundance of insect larvae ($F_{(2,39)} = 8.038$, $P = 0.001$) fed to chicks between years. In 2001 there were significantly more insect larvae (weighted mean 0.529 ± 0.107 , $n = 15$) present in skylark chick diet than in 2000 (weighted mean 0.188 ± 0.085) and 2002 (weighted mean 0.212 ± 0.113). Fewer araneae and coleoptera were fed to chicks in 2001 than in 2000 and 2002 but after a Bonferroni correction was applied this was not significant (Figure 1a).

No significant differences in skylark chick diet were detected between months or with age for any of the invertebrate groups tested. However, Figure 1b shows that skylark chicks were fed more insect larvae in May ($F_{(2,39)} = 3.467$, $P = 0.041$, weighted mean 0.524 ± 0.136 , $n = 14$) than June or July ($F_{(2,39)} = 3.985$, $P = 0.027$, weighted means 0.305 ± 0.096 , $n = 11$ and 0.246 ± 0.095 , $n = 17$ respectively) and fewer 'other insects' (weighted mean May 0.028 ± 0.02 , June 0.150 ± 0.10 and July 0.205 ± 0.063) despite the result being non-significant after Bonferroni correction.

5.4.2.2 Yellowhammers

Data from 15 broods and 20 samples were included in the analysis. After a sequential Bonferroni correction was applied, there was a significant difference in 'other insects' present in yellowhammer chick diet between months ($F_{(2,17)} = 7.762$, $P = 0.004$). There were significantly more 'other insects' in August (weighted mean 0.385 ± 0.305 , $n = 3$) than June (weighted mean 0.095 ± 0.068 , $n = 9$) or July (weighted mean 0.021 ± 0.038 , $n = 8$). Figure 1c shows that more coleoptera were fed to chicks in June (weighted mean 0.279 ± 0.133 , $n = 9$) than July or August (weighted means 0.028 ± 0.045 , $n = 8$ and 0.037 ± 0.031 , $n = 3$ respectively) but once the Bonferroni correction was applied this difference was not significant ($F_{(2,17)} = 3.678$, $P = 0.047$, ns). There was no significant difference in yellowhammer chick diet between the two age groups for any of the six invertebrate groups tested.

5.4.2.3 Song thrushes

Throat samples

Data from 18 broods and 21 samples were included in the analysis. There were no significant differences in song thrush chick diet between years, between months or between the two age groups for any of the six invertebrate groups tested.

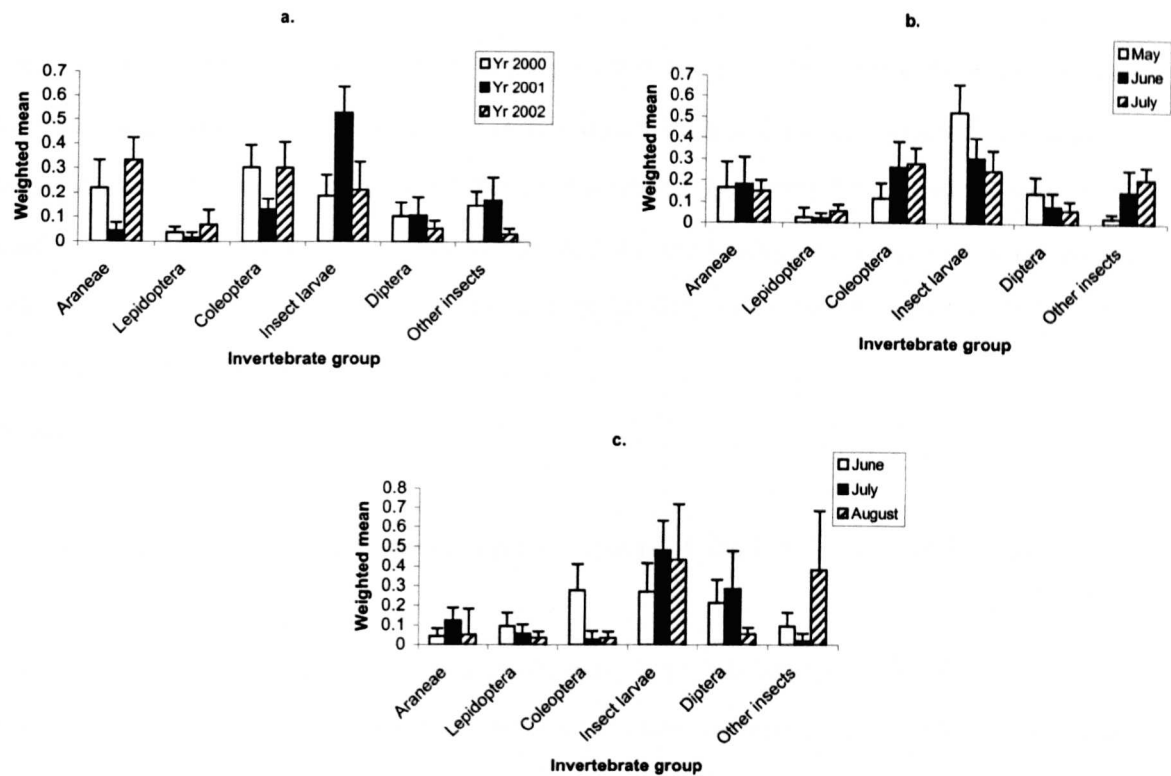


Figure 1: Weighted mean densities of different invertebrate groups present in (a.) skylark chick diet across years 2000-2002 and (b.) month and (c.) yellowhammer chick diet across months, ± 1 SE.

Faecal samples

Data from 50 samples and 44 broods were included in the analysis. There were no significant differences in song thrush chick diet between years, between months or between the two age groups for any of the seven invertebrate groups tested.

5.4.3 Chick diet and invertebrate availability

5.4.3.1 Skylarks

Throat samples and invertebrate availability data were available for 23 nests (7 in 2000, 11 in 2001 and 5 in 2002). Figure 2 shows the mean proportion of the different invertebrate groups in neck ligature samples and D-vacuum samples.

There was no significant year effect (Wilk's lambda = 0.740, $F_{(5,17)} = 1.194$, $P = 0.353$) or month effect (Wilk's lambda = 0.641, $F_{(5,17)} = 1.903$, $P = 0.147$) on skylark chick diet relative to invertebrate abundance. Results showed that the composition of chick diet samples differed significantly from that of the invertebrates found at foraging sites around the nests. Provisioning skylarks were feeding their chicks significantly more of some invertebrate groups than others, relative to their availability, at their foraging sites (Wilk's lambda = 0.038, $F_{(5,18)} = 90.734$, $P < 0.001$).

The simplified ranking matrix,

Insect larvae >> Araneae > Other insects+lepidoptera adults > Coleoptera >>> Diptera >> Parasitica,

shows that several invertebrate taxa were selected for more than would be expected by provisioning adults (Table 8). Insect larvae were significantly selected over all other invertebrate groups, followed by araneae. Coleoptera were fed to nestlings significantly more than diptera and parasitica, but less than expected relative to availability (Figure 2). Diptera and parasitica, the lowest ranking invertebrate groups, were fed to chicks significantly less than would be expected relative to their availability. Parasitica were not taken by provisioning adults for chick food even though they were numerous at foraging sites (Figure 2).

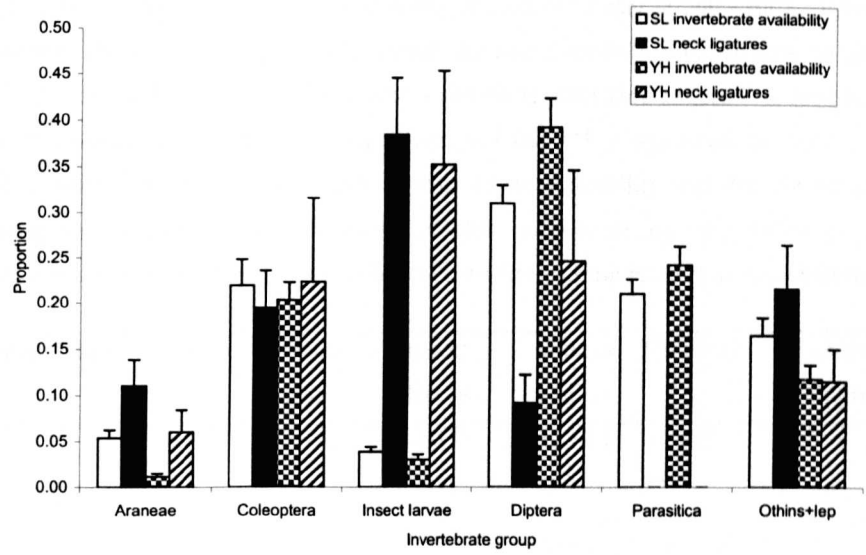


Figure 2: Mean invertebrate availability at skylark (SL) and yellowhammer (YH) foraging sites and invertebrates in neck ligature samples from skylark and yellowhammer chicks, \pm 1SE.

Table 8: Log ratio difference matrix for examining *skylark chick diet* in 2000-2002. Invertebrates from D-vacuum samples taken from foraging sites around the nest constitute invertebrates 'available' to foraging birds and invertebrates from neck ligature samples constitute invertebrates 'used' to feed nestlings. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the invertebrate group used most relative to its availability and the lowest rank indicates the invertebrate group used least relative to its availability. A positive log ratio difference indicates the row invertebrate group was used more than the column invertebrate group relative to its availability.

Invertebrate Group	Araneae	Coleoptera adults	Insect larvae	Diptera adults	Parasitica	Other insects + lepidoptera adults	Rank
Araneae	-	+0.979 ns	-2.151 *	+3.819 ***	+7.955 ***	+0.576 ns	2
Coleoptera adults	-0.979 ns	-	-3.447 **	+3.077 **	+7.499 ***	-0.287 ns	4
Insect larvae	+2.151 *	+3.447 **	-	+6.794 ***	+11.678 ***	+2.688 **	1
Diptera adults	-3.819 ***	-3.077 **	-6.794 ***	-	+3.254 **	-3.791 ***	5
Parasitica	-7.955 ***	-7.499 ***	-11.678 ***	-3.254 **	-	-7.753 ***	6
Other insects + lepidoptera adults	-0.576 ns	+0.287 ns	-2.688 **	+3.791 ***	+7.753 ***	-	3

5.4.3.2 Yellowhammers

Throat samples and invertebrate availability data were available for 12 nests in 2000 (7 in June and 5 in July). Due to time constraints invertebrate samples were not analysed for May and August so data from these nests were excluded from the analysis.

Figure 2 shows the mean proportion of the different invertebrate groups in throat and D-vacuum samples. There were no significant month effects (Wilk's lambda = 0.557, $F_{(5,6)} = 0.954$). Results showed that the composition of neck ligature samples differed significantly from that of the invertebrates found at foraging sites around the nests. Yellowhammers were taking significantly more of some invertebrate groups than others relative to their availability at their foraging sites (Wilk's lambda = 0.029, $F_{(5,7)} = 46.979$, $P > 0.001$). The simplified ranking matrix,

Insect larvae > Araneae > Other insects+lepidoptera adults > Coleoptera > Diptera > Parasitica,

shows that insect larvae and araneae, the highest ranking invertebrate groups, were selected for more than would be expected relative to their availability by provisioning adults. Diptera and parasitica, the lowest ranking invertebrate groups, were fed to chicks less than would be expected relative to their availability by provisioning adults (Table 9). Parasitica were not taken by provisioning adults for chick food even though they were numerous at foraging sites (Figure 2).

5.4.3.3 Skylark and yellowhammer comparison

There was no significant difference in skylark and yellowhammer chick diet composition between months (Wilk's lambda = 0.710, $F_{(5,13)} = 1.063$, $P = 0.424$) and there was no significant difference in chick diet composition of skylark and yellowhammer nestlings (Wilk's lambda = 0.664, $F_{(5,13)} = 1.313$, $P = 0.318$). Skylarks and yellowhammers fed their nestlings a very similar diet from what was available around their nest sites.

Figure 2 shows that parasitica were never found in neck ligature samples of either skylark or yellowhammer nestlings, despite being numerous at foraging sites. Skylarks and yellowhammers fed fewer diptera than expected relative to availability. Both species fed insect larvae followed by araneae more than expected relative to availability. Skylarks fed more other insects+lepidoptera larvae to chicks and yellowhammers fed more coleoptera to chicks than did skylarks.

Table 9: Log ratio difference matrix for examining *yellowhammer chick diet* in 2000. Invertebrates from D-vacuum samples taken from foraging sites around the nest constitute invertebrates 'available' to foraging birds and invertebrates from neck ligature samples constitute invertebrates 'used' to feed nestlings. Ns – not significant, * = significant at 0.05, ** = significant at 0.01, *** = significant at 0.001. The highest rank indicates the invertebrate group used most relative to its availability and the lowest rank indicates the invertebrate group used least relative to its availability. A positive log ratio difference indicates the row invertebrate group was used more than the column invertebrate group relative to its availability.

Invertebrate Group	Araneae	Coleoptera adults	Insect larvae	Diptera adults	Parasitica	Other insects + lepidoptera adults	Rank
Araneae	-	+1.478 ns	-0.888 ns	+3.376 **	+8.069 ***	+1.299 ns	2
Coleoptera adults	-1.478 ns	-	-1.954 ns	+1.266 ns	+4.017 ***	-0.673 ns	4
Insect larvae	+0.888 ns	+1.954 ns	-	+2.805 **	+6.882 ***	+1.975 ns	1
Diptera adults	-3.376 ± 0.959 **	-1.266 ± 1.641 ns	-2.805 ± 1.464 **	-	+2.141 ± 0.994 ns	-1.512 ns	5
Parasitica	-8.069 ***	-4.017 ***	-6.882 ***	-2.141 ns	-	-5.678 ***	6
Other insects + lepidoptera adults	-1.299 ns	+0.673 ns	-1.975 ns	+1.512 ns	+5.678 ***	-	3

5.4.4 Chick growth

Species growth curves were plotted using mean weight and tarsus measurements from all chicks measured in each brood (open squares, Figure 3a - f). A second curve was plotted onto this that excluded any measurements that were taken after a brood experienced partial chick loss (closed squares). Graphical representation of weight and tarsal development (Figure 3a - f) show that for skylark and yellowhammer, mean chick weight and tarsus measurements are marginally less when broods that have experienced chick loss are included. Broods that lose chicks may possibly be subjected to pressures such as food limitations, so a lower growth curve may be expected than those broods that do not lose chicks. Alternatively brood reduction could increase brood means as the remaining siblings gain more food and hence increase growth rate. The two song thrush growth curves are very similar, which may mean parent birds can compensate for brood losses.

For each species, the curves of weight and tarsus are similar. It is clear that weight and tarsus growth for skylark and song thrush plateau out near to the time that chicks leave the nest; for skylarks between 8 - 10 days and for song thrush around day 9. Not enough data were collected from yellowhammer broods over the course of a single breeding season in 2000 to elaborate on any patterns of growth and development. For analysis of chick growth, data excluding the loss of individuals in a brood were therefore taken into account in an attempt to eliminate bias.

5.4.4.1 Skylark chick growth rates

Data from 26 nests with more than one set of biometric measurements and excluding nest data where chicks died were included in the analysis.

Skylark chick growth rate using mass

Results from the analysis using *GR 1* data showed none of the variables tested affected chick body weight gain per day. *GR total* data analysis showed nest outcome and the proportion of set-aside around the nest had significant univariate effects on weight gain per day (Table 10). Growth rate was significant and positively related to the proportion of set-aside around the nest, explaining 28.1% of variance. Nests that successfully

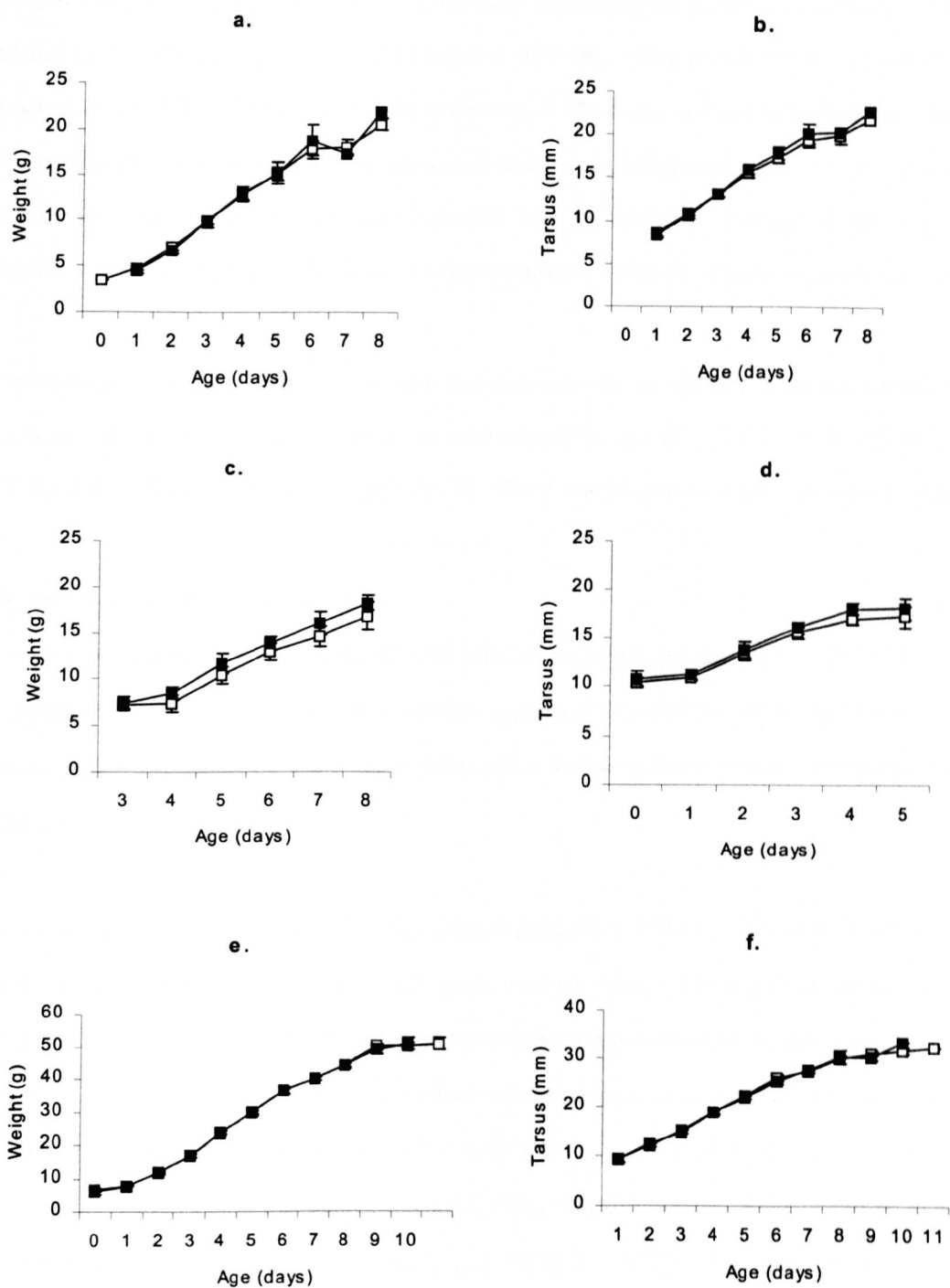


Figure 3: Visual representation of growth measurements using mean weight (g) and tarsus (mm) $\pm 1SE$. Open squares are calculated from all biometric measurements collected from each brood (weight or tarsus), for skylark ($n = 44$) (a and b), yellowhammer ($n = 21$) (c and d) and song thrush ($n = 102$ broods) (e and f) chicks in the nest. Closed squares represents data collected excluding measurements taken once partial brood loss had occurred, for skylark ($n = 26$ and 22 broods) (a and b), yellowhammer and ($n = 11$ and 11) (c and d) and song thrush ($n = 55$ and 49 broods) (e and f).

fledged young have higher growth rates than those that did not, explaining 29.9% of variance. The proportion of araneae in nestling diet had a significant negative effect on nestling growth rate ($F_{(1,17)} = 6.01$, $P = 0.025$, slope estimate -3.37 ± 1.38 , $t_{(17)} = 2.45$) explaining 21.8% of the variance in growth rate. The effect of invertebrate abundance around the nest approached statistical significance ($F_{(1,17)} = 3.81$, $P = 0.068$), inferring that the lower the invertebrate abundance around the nest, the lower the chick growth rate (slope estimate -0.876 ± 0.449 , $t_{(17)} = 1.95$). Invertebrate abundance explained 13.5% of variance in growth rate.

The minimum adequate model (MAM) that best describes the growth rate using the variables examined included both outcome and proportion of set-aside around the nest ($F_{(2,22)} = 11.76$, $P < 0.001$), explaining 47.3% of the variance in growth rate (g) (Table 10). There was no interaction between the two variables.

Skylark chick growth rate using tarsus

Clutch size was the only variable to significantly affect tarsus length gain per day ($F_{(2,23)} = 3.82$, $P = 0.037$, $R^2 = 18.4\%$), in the *Tarsus 1* analysis. This was also significant as a quadratic term. There was an increase in tarsus growth rate between 2 and 3 egg clutches and a decline in tarsus growth rate between 3 and 4 egg clutches.

Univariate analysis from the *Tarsus total* data set showed that four of the variables were significant (Table 10). Both brood and clutch size were also significant as quadratic terms. Tarsus growth rate increased between clutch and brood sizes of 2 and 3 eggs or chicks and declined between clutch and brood sizes of 3 and 4 eggs or chicks. Clutch size and brood size significantly affected tarsus growth rates, explaining 40.5% and 20.4% of the variance respectively ($F_{(2,23)} = 9.50$, $P < 0.001$ and $F_{(2,23)} = 4.20$, $P = 0.028$). Tarsus growth rate of successfully fledged chicks was significantly greater than those that did not fledge. Outcome explained just 14.9% of the variance in tarsus growth rate ($F_{(1,24)} = 5.38$, $P = 0.029$). Tarsus growth rate was negatively influenced by the proportion of 'other' habitats around the nest ($F_{(1,23)} = 7.77$, $P = 0.01$), explaining 22% of the variance in tarsus growth rate. Other habitats not surprisingly included permanent pasture, woodland, hedges, ditches, riparian habitats and buildings and gardens. Diet composition did not affect skylark nestling tarsus growth rates.

The best-fit MAM to describe the data included clutch size and the proportion of 'other' habitats around the nest, ($F_{(3,21)} = 10.03$, $P < 0.001$, $R^2 = 53\%$)

Table 10: Results from univariate and multivariate models on skylark chick growth rates (using weight and tarsus). Explanatory variables are described in Table 4. *GR total* and *tarsus total* is the mean difference in weight or tarsus length between the first and last biometric measurement taken divided by the days spanned. Signs in parentheses show the direction of change in the growth rate with an increase in the explanatory variable.

Variables	Skylarks <i>GR total</i>		Skylarks <i>Tarsus total</i>	
	Univariate	Multivariate	Univariate	Multivariate
<i>Mean age</i>	ns	ns	ns	ns
<i>Year</i>	ns	ns	ns	ns
<i>Clutch size</i>	ns	ns	$F_{(2,23)} = 9.50$, $P < 0.001$ (-)	$F_{(2,21)} = 11.69$, $P < 0.001$ (-)
<i>Brood size</i>	ns	ns	$F_{(2,23)} = 4.20$, $P = 0.028$	ns
<i>Outcome</i>	$F_{(1,24)} = 11.66$, $P = 0.002$ (+)	$F_{(1,1)} = 15.35$, $P < 0.001$ (+)	$F_{(1,24)} = 5.38$, $P = 0.029$ (+)	ns
<i>Invertebrate abundance</i>	$F_{(1,17)} = 3.81$, $P = 0.068$, ns (-)	ns	ns	ns
<i>Foraging distance from nest</i>	ns	ns	ns	ns
<i>Proportion of set-aside</i>	$F_{(1,23)} = 10.37$, $P = 0.004$ (+)	$F_{(1,22)} = 8.18$, $P = 0.009$ (+)	ns	ns
<i>Proportion of 'other' habitats</i>	ns	ns	$F_{(1,23)} = 7.77$, $P = 0.010$ (-)	$F_{(1,21)} = 6.71$, $P = 0.017$ (-)
<i>Proportion araneae</i>	$F_{(1,17)} = 6.01$, $P = 0.025$ (-)	ns	ns	ns
<i>Rainfall</i>	ns	ns	ns	ns
<i>Inc mean</i>	ns	ns	ns	ns
<i>Month</i>	ns	ns	ns	ns
<i>Predator control</i>	ns	ns	ns	ns
<i>Farm C/B</i>	ns	ns	ns	ns
<i>Habitat</i>	ns	ns	ns	ns
<i>Date of last egg</i>	ns	ns	ns	ns
<i>Month young in nest</i>	ns	ns	ns	ns
<i>Young mean (mean temperature over a 5 day period prior to hatching)</i>	ns	ns	ns	ns
<i>Cover density at nest</i>	ns	ns	ns	ns
		$R^2 = 47.3\%$		$R^2 = 53\%$

5.4.4.2 Yellowhammer chick growth rates

The variables measured showed no effect on yellowhammer chick weight or tarsus growth rates. This is likely to be due to the fact that once nests that did not reach the analysis requirements were excluded only 11 nests were available for analysis. The analysis was repeated for nests with more than one measurement taken but without controlling for partial brood loss ($n = 21$).

Yellowhammer chick growth rate using mass

No significant effects of the variables were recorded on yellowhammer chick growth rates (g) using data from *GR total*. However, brood size negatively affected growth rates (g) although this result only approached significance ($F_{(3,12)} = 3.09$, $P = 0.068$, $R^2 = 29.5\%$) when using data from *GR 1*.

Yellowhammer chick growth rates using tarsus

No significant effects of the variables tested were recorded on yellowhammer chick tarsus growth rates (mm) using data from *Tarsus 1*. Using data from *Tarsus Total* the mean temperature over a five-day period whilst chicks were in the nest had a significant effect on tarsus growth rates ($F_{(1,6)} = 7.48$, $P = 0.034$, $R^2 = 48.1\%$). As temperature increased chick tarsus growth rates decreased (slope estimate -0.226 ± 0.082 , $t_{(6)} = 2.73$).

5.4.4.3 Song thrush chick growth rates

Data from 52 nests, with more than one set of biometric measurements and excluding nests where chicks died, were included in the analysis.

Song thrush chick growth rates using mass

Results from analysis using *GR 1* data showed that chick age had a significant positive effect on growth rate ($F_{(2,50)} = 10.98$, $P = 0.002$). This explained 16.4% of the variance of growth. No other variable tested significantly affected song thrush chick weight with this analysis.

Results from analysis using *GR total* data showed that the date song thrush incubation commenced (date of last egg) had a weak negative correlation on chick weight gained per day ($F_{(1,49)} = 4.43$, $P = 0.041$, $R^2 = 6.4\%$, slope estimate = -0.002 ± 0.001 , $t_{(49)} = 2.10$). As the breeding season progressed chick growth rate (g) declined. Interestingly, the proportion of permanent pasture around a nest had a weak positive association with growth rate (g) but this was not significant ($F_{(1,50)} = 3.55$, $P = 0.065$), explaining only 4.8% of the variance in growth rate. There was also weak evidence of a decline in growth rate (g) when no predator control was taking place ($F_{(1,50)} = 3.77$, $P = 0.058$), explaining only 5.1% of the variance in growth rate.

Age had no significant effect on growth rate in this analysis, unlike that using data from *GR 1*.

Song thrush chick growth rates using tarsus

No significant effects of the different variables were found on song thrush chick tarsus growth rate using the data set *Tarsus 1*. Chick age was the only variable tested that had a weak significant negative relationship on tarsus growth rate using the *Tarsus total* data set ($F_{(1,43)} = 5.47$, $P = 0.024$, $R^2 = 9.2\%$, slope estimate -0.235 ± 0.100 , $t_{(43)} = 2.34$).

5.5 Discussion

5.5.1 General foraging watch observations

No statistical analysis was carried out on the following behavioural observations that were made. Over the course of the study period skylarks were always observed foraging on the ground. They were frequently observed digging in the soil, turning over stones, moving grass aside and pulling insects from the ground, particularly in newly sown set-aside or in bare patches within the set-aside strips. It was no surprise that chicks were fed larvae and pupae that may have been in the ground or well hidden in vegetation such as beetle banks. Tipulidae pupae were taken in considerable amounts and insect larvae were taken more than would be expected relative to their availability.

Female skylarks would collect food, return to the nest and brood for a few minutes until the male returned. He would leave when she returned. Female skylarks appeared to forage closer to the nest than males, although no

data were collected to confirm this observation. When chicks were older, both parents made frequent regular visits to the nest and females spent less time brooding unless it was raining heavily or it was particularly hot. In very hot weather, or close to the middle of the day, neither parent foraged as regularly. The female would stay at the nest and brood the chicks and the male would be seen walking around close to the nest or perched nearby singing. During prolonged periods of heavy rain, female skylarks were also observed foraging for chick food, leaving nests unattended. Obviously the parental role of protecting young from the elements and providing food in this situation means making the choice between preventing young starving and chilling. Dead chicks were only removed from the nest by a parent if they were small and therefore light. Dead, older and heavier chicks often remained in the nest. Pairs from neighbouring territories would forage in the same areas without fighting, but if either approached the vicinity of the other's nest a chase or fight would ensue.

For both skylarks and yellowhammers, the female appeared to be the main provider of chick food. The males spent more time singing or defending the territory when nestlings were small and were never observed brooding the chicks. In one instance a female skylark was killed whilst on the nest and the young starved. The male made no attempt to bring them up alone and they died only a day later. Another instance recorded a male skylark disappearing from his territory and the female trying to bring up the chicks alone. She failed by day seven when they were found dead from starvation. The female disappeared from the territory, either abandoning the nest attempt to start elsewhere or having been predated. In this situation the male's contribution could have helped meet the demands on the growing brood.

In contrast to the skylark, yellowhammers were observed foraging on the ground for insects and on cereal crops for grain. For yellowhammers, which were studied for a single breeding season, several observation periods did not record more than five foraging trips in 90 minutes. Chicks grew slowly and most broods experienced partial brood loss through starvation. This contributed to the reasons for not continuing the yellowhammer study in further years. Generally males did not provision young and spent a lot of time perched in the hedges next to the nest singing. During heavy rain, female yellowhammers sat tightly on their brood and tended not to come off and forage at all. One female brooded dead chicks for several days before the author removed them.

Song thrushes were only seen foraging if they were in an open habitat such as permanent pasture or within gardens. They were sometimes flushed from ditches and hedges carrying food. The male of this species carries out most of the provisioning duties whilst the female stays at the nest (Hartley, 1967). Covering areas up to at least a few square metres, birds were often seen cocking their head to the ground as if listening for movement in the vegetation or in the soil. They carried a full beak of prey items straight back to the nest at any one time and generally foraged in a single habitat at a time.

5.5.2 Nestling diet

5.5.2.1 Skylarks

Unripe grain was fed to skylark chicks in each year of this study (29% of all broods were fed it). This has not previously been recorded in other studies although it is a main constituent of the adult diet (Green, 1980; Tryjanowski, 1995). Regurgitated seeds are also cited as part of the nestling diet after 7 days old (Simms, 1992), although they were not found in the current study. It has been speculated that grain present in corn bunting nestling diet is a poor substitute for invertebrate prey, reflecting a lack of available invertebrate prey items (Watson, 1992). The result in the current study may be due to local effects, although it demonstrates that skylark diet is adaptable to local prey availability.

This study reported high proportions of insect larvae (fed to 75% of all broods), araneae (fed to 71% of broods) and coleoptera (64%) in chick diet. Donald et al. (2001d) found larvae occurred less in the diet of skylark nestlings in southern England, in 36.4% of faecal sacs, although araneae occurred more (92.4% of faecal sacs) and also coleoptera (27.3-66.7% of faecal sacs). Donald et al. (2001d) also found that insect larvae were the only insect group to affect chick body condition, which was higher in broods fed larvae than those that were not fed larvae. Poulsen et al. (1998) found more larvae in the diet of young chicks, up to 5 days old, which then shifted to more coleopterans. The current study found that the proportion of araneae in the diet affected growth rates (g/day) and growth rates were lower in broods with a higher proportion of spiders in the diet. Why this is so remains unknown. If there was a super abundance of spiders and adults

were feeding them to chicks in preference to other nutritionally valuable invertebrates, because they were easier to catch or handle, then chicks may be lacking in certain nutrients.

Orthopterans were an important part of skylark chick diet in the study by Jenny (1990b) in Switzerland but not by Weibel (1999). Donald et al. (2001d) found only broods in set-aside were fed them in his study. No orthopterans were found in neck ligature samples in this study, although they are present in beetle banks, verges and field margins at Loddington (Chris Stoate, Pers. comm.). More use of diptera was made in this study (with 41% of broods being fed this group) than in Donald et al's (2001d) study (13.6% occurrence in faecal samples). Jenny (1990b) also found a high use of diptera in nestling diet. In the present study, mainly adult tipulidae, which are generally slow flying and easy to catch, were fed to skylark chicks. Hymenoptera adults were not utilised by foraging adults, even though they were abundant at foraging sites. This result is in contrast to Poulsen & Aebischer (1995) who found high mean proportions of hymenoptera adults in both skylark neck ligature and faecal samples when examining chick diet. Most parasitic wasps are likely to be too small a prey item for skylarks to take and along with the larger adult sawfly were not recorded in neck ligature samples at Loddington. Weibel (1999) found that hymenopterans made up 15% of the diet in his study, which also used neck ligatures to gather dietary samples, and that the proportion of hymenopterans in the diet increased with chick age as the proportion of araneae and lepidoptera decreased.

In relation to available coleoptera at Loddington, provisioning skylarks were not selecting coleoptera more than would be expected relative to their availability. Coleoptera were however found in 64% of broods diet (from neck ligature samples) so form an important role in nestling diet. Most beetles fed to chicks were medium to large carabids, generally over 0.5cm in size. This analysis did not take beetle size into account and it is possible that the sampling technique picked up small but not large beetles, biasing results. Elmegaard et al. (1999) found, in Denmark, that ground beetles were the primary prey item fed to skylark nestlings and that the abundance of them was not affected by being exposed to full pesticide treatment. In fields that had been subjected to a reduced pesticide treatment, nestling diet was more diverse than that of nestlings in fields exposed to full pesticide treatments. Since some beetle species are less sensitive to pesticide application than a whole host of other invertebrates (Wilson et al., 1999) this may then explain the difference in diet. In the current study, araneae were selected relatively more than would be expected from their availability. They are

susceptible to pesticide applications (Wilson et al., 1999) so may be present in greater abundance in the non-cropped habitats than in crops where skylarks tend to forage. Since there is less pesticide application in these habitats, this may reflect skylarks habitat use at Loddington.

No changes in skylark nestling diet were detected with age in this study, contrary to Poulsen et al. (1998), Weibel (1999) and Donald et al. (2001d). Testing between different age groups may have been more sensitive in detecting changes in diet with age, but in the present study the limited sample size at each age (days) restricted possible age group comparisons. Evans et al. (1997) recorded different diets between late and early season cirl bunting chicks, with earlier broods being fed more orthopterans than late broods, but Brickle & Harper (1999) detected no change in corn bunting nestling diet with age. In the current study, there was a significant difference in the amount of insect larvae present in chick diet between years, with more recorded in the diet in 2001 than in 2000 or 2002, perhaps reflecting local changes or inter-annual availability. The investigation of change in skylark chick diet with chick age showed skylarks were fairly consistent in what they fed their chicks over the course of a breeding season. This was further supported by the results that demonstrated that skylarks fed chicks significantly more of some invertebrate groups than others relative to what was available at foraging sites.

5.5.2.2 Yellowhammers

Yellowhammer dietary preferences in this study were similar to those found by MacCleod (2001) in Scotland and Stoate et al. (1998), also at Loddington. Insect larvae in the current study were strongly selected for in nestling diet, particularly tipulidae pupae, relative to availability. Although Stoate et al. (1998) found lepidoptera larvae in 81.5% of broods, this study recorded their occurrence in 30% of broods ($n = 20$). Differences could possibly be accounted for in annual differences in availability and may also have contributed to the poor breeding success in this year of study.

Relative to availability, araneae were an important prey group (fed to 35% of all broods) although they only formed 5% of invertebrates by number. In contrast, diptera, while fed to 45% of all broods, were fed less than expected relative to their availability. This could be because all diptera in the D-vacuum suction samples were

counted and the group included the largest and the smallest dipterans present. Analysis should have accounted for large and small diptera, and then perhaps differences in their general use might have been detected. 'Other insects and lepidoptera adults' ranked third relative to availability but this could be due to the large number of invertebrate groups combined. Hymenoptera adults were not utilised by foraging adults even though they were abundant at foraging sites. Most parasitic wasps are probably too small a prey item for yellowhammers. No adult sawfly was recorded in their diet at Loddington.

Provisioning yellowhammers were consistent in their choice of prey items fed to chicks across the nestling period as diet did not change with age. This is in agreement with Stoate et al. (1998) on the same study site, between 1993 and 1997. Results from compositional analysis of chick diet and invertebrate availability also supported this finding as there was no effect of month on prey type selection relative to availability and insect larvae and spiders were strongly selected for. Chicks were fed significantly more 'other insects' in August compared to June and July and this could be attributed to an increase in the availability of 'other insects' and a decrease in insect larvae and other groups.

5.5.2.3 *Song thrushes*

Song thrushes were consistent in what they fed their chicks regardless of age, month or year with the major components of diet comprising earthworms and gastropoda. Both faecal and neck ligature samples were in agreement with this although, due to the limitations in sampling techniques (discussed later), faecal samples may have provided a better representation of what was fed to chicks, recording 97% of all broods being fed earthworms and 76% gastropoda. Faecal samples also detected higher occurrences of other invertebrate groups than neck ligature samples did. This may be a true reflection of their varied diet across a longer time frame (Hartley, 1948; Drycz, 1969; Simms, 1978; Török, 1985; Gruar et al., 2003). Hill et al. (1999b) recorded a steady increase in the number of feeds per hour with song thrush chick age, starting at around 5 visits per hour at the age of 4 days old. Neck ligatures in the current study were left on for up to 50 minutes so one would have expected the sampling technique to be more productive than it was. This may indicate that adult birds ate the prey brought to the nest or that the ligatures disturbed their normal provisioning behaviour.

Earthworms have been recorded in many other studies as the major dietary component and a switch to snails is apparent in many of the studies over the breeding season when earthworm availability drops (Davies & Snow, 1965; Schnäck, 1991; Gruar et al., 2003 etc) as worms move deeper into the ground as the soil gets harder. Snail shell was detected in a large quantity of faecal samples and it has been suggested that the shell is a good source of calcium for bone development (Graveland, 1995 as cited in Wilson et al., 1997b).

Studies across central European woodlands; Hungary (Török, 1985), Poland (Drycz, 1969) and Vienna (Schnäck, 1991), showed that song thrush nestlings took a large proportion of caterpillars, flies and beetles in their diet. The current study did not record caterpillar larvae in nestling diet, despite caterpillars being available at the study site, and Gruar et al. (2003) recorded only small amounts (6 - 8%) in the Essex and Sussex study. Differences in diet are likely to be due to invertebrate availability at the site level.

5.5.3 Growth rates

Measure of growth rates

Factors affecting chick growth rates are numerous, including environmental, parental condition or experience and seasonal effects. The effects of some of these factors on chick growth rates were examined within this study. Using the shortest consecutive time period to measure growth rates, whether using tarsus or weight, may be too small a time period to detect any genuine changes due to environmental factors or others. In this project chicks in a brood were sometimes measured daily; possibly too brief a snapshot in time, although this procedure would demonstrate short term fluctuations, for example in response to a day of heavy rain. Using the first and last measurement to calculate growth rate proved to be a better means of detecting the influence of various factors on growth rates during the nestling period. Growth rates documented over an extended nestling period could help provide important information on chick condition. Reduced growth rates could result in chicks taking a longer time to leave the nest, thereby increasing the risk of brood predation. Subsequently, chicks that fledge at lower weights might experience reduced post-fledging survival (Magrath, 1991; Grubb et al., 1998; Naef-Daenzer et al., 2001).

Effects of habitat availability on growth rates

On farmland the different habitats provide different degrees of shelter, food availability, nesting, breeding, foraging and over wintering grounds for many species. During the breeding season the habitats available to provisioning birds may have varying effects on chick growth rates, which in turn may lead to the success or failure of the nest.

For skylarks, nestling growth rates (g/day) were higher as the proportion of set-aside around the nest increased and tarsus growth rates (mm/day) were lower as the proportion of 'other habitats' around the nest increased. Skylarks mainly feed their chicks invertebrates and, within Loddington, forage for them in set-aside (Chapter 3). Set-aside at Loddington was mainly non-rotational and was present across the farm in strips creating a mosaic of habitats for many territories in an otherwise homogeneous environment. Set-aside receives little or no pesticide treatment during the breeding season and is therefore a reservoir for invertebrates, particularly insect larvae, which ranked highest in nestling diet. Donald et al. (2001d) found that skylarks nesting in set-aside frequently provided their chicks with insect larvae, and these had a significant positive effect on body condition. Skylarks are known to avoid boundary features such as field margins along hedges (Buckingham, 2001), even though these habitat types also support a large number of potential prey items. 'Other habitats', including buildings, permanent pasture, riparian habitats, woodland, hedges and ditches, are also areas that skylarks avoid. Higher proportions of these habitat types around nests could firstly, reduce the amount of area available for foraging and secondly, potentially increase the amount of interference by man or predators, both of which could directly and indirectly affect growth rates of nestlings. Skylark nestlings with higher growth rates (g/day and mm/day) were more likely to fledge successfully, so the availability of high quality foraging habitats around the nest, such as managed set-aside, may affect their success rate.

Skylarks in this study generally foraged a mean distance of $50\text{m} \pm 1.4\text{m}$ from the nest. Poulsen et al. (1998) recorded mean foraging distance in different crop types between 120 – 270m (which decreased with chick age), whilst Donald (1999) recorded mean foraging distance in Southern England as $75\text{m} \pm 4.1\text{m}$. As suggested by Donald (2004), these differences in foraging distances may be due to local conditions, such as suitable foraging habitat or food availability and abundance. If set-aside is positioned in strips across the farm,

as is the case at Loddington, birds may have to travel a shorter distance to forage there than if a whole field was turned over to set-aside. Set-aside strips may result in a lower cost to the provisioning adult and perhaps more provisioning trips could be made. In this study, total invertebrate abundance around skylark nests did not significantly affect growth rates but inferred that the lower the abundance around the nest, the lower the nestling growth rates. Surprisingly, invertebrate abundance around nest sites did not significantly affect growth rates for any of the study species. Not all nests included in the analysis had a measure of invertebrate abundance calculated, since not all nests were involved in foraging watches, so it is quite likely that invertebrate abundance and its affect on chick growth rates was inadequately investigated in this study. Brickle et al. (2000) found in his study of corn bunting nestling diet that chick weight, when corrected for age with tarsus length, was positively correlated with invertebrate abundance around the nest.

The proportion of different habitat types around the nest did not influence yellowhammer and song thrush chick growth rates in this study. It should be noted that the yellowhammer data set covered only a single breeding season and was very small, so results from this analysis may not be representative and should be treated with caution. However, the amount of permanent pasture around song thrush nests was (weakly) positively correlated with growth and this also affected nest survival during the incubation stage (see results in Chapter 2). Grassland habitats are known to have more earthworms than arable land (Edwards & Lofty, 1982; Tucker, 1992), which could benefit song thrush chick growth rates if most nests had access to pasture as a foraging ground.

Effects of weather on growth rates

Previous studies have shown that weather can significantly affect chick growth and development. Donald et al. (2001d) found that rainfall was negative correlated with nestling skylark growth rates. Bradbury et al. (2003) also found this and that the number of hours of sunshine and an increase in minimum temperature had a positive effect on skylark, yellowhammer and chaffinch nestling growth rates. In the current study, mean temperature over a 5 - day period when yellowhammer chicks were in the nest was found to have a significant negative effect on tarsus growth rates, only when including data from all nests without excluding those experiencing partial brood loss. High temperatures could affect invertebrate movements, making them harder

for provisioning adults to find or catch, or parent birds may spend more time on the nest protecting young from the heat rather than providing food. Observations from this study showed that, during the hottest parts of the day parent bird activity was reduced. Females seemed to spend more time on the nest and males spent less time singing. The year 2000 was recorded as the wettest summer on record for 100 years. Surprisingly, the amount of rainfall was not correlated with growth rates of any of the three study species although many broods experienced partial brood loss from starvation which could quite feasibly have been brought about by the trade off between foraging for chick food or brooding young. Invertebrate activity was also likely to be reduced by rainfall, making them harder to locate so ripening grain probably became a more important food source (Stoate et al., 1998; MacCleod, 2001).

Weather was not found to significantly affect growth rates of skylark and song thrush nestling chicks, contrary to Donald et al. (2001d), Bradbury et al. (2003) and Gruar et al. (2003). The first two studies also investigated the effects of hours of sunshine and minimum and maximum temperatures, factors that this study did not examine.

Effects of outcome (success or failure)

Successful fledging skylark chicks had significantly higher growth rates (g/day) than those that did not fledge and as shown in Chapter 2, this significantly affected nestling survival. This was not true for yellowhammers or song thrushes. Successful fledging skylark chicks also had significantly higher tarsus growth rates. For this species it is not a surprising result since they leave the nest early between 8 - 10 days old. Rapid tarsus development is necessary in order for them to be able to leave the nest and survive while still flightless. Bradbury et al. (2003) found in their study of linnet (*Carduelis cannabina*), chaffinch (*Fringilla coelebs*), skylark and yellowhammer growth rates that none of the broods that suffered predation had significantly lower growth rates or poorer body condition than successful broods. The present study however, never investigated the difference in growth rates of starved or predated broods. Nevertheless, skylark chicks with lower growth rates had a less likely chance of fledging. This could be attributed to a number of reasons.

Firstly, there could be an increase in the amount of begging. As the skylark is a ground nesting species, ground predators may be able to pinpoint the noise of the chicks, hence increasing the rate of predation. Indeed Evans et al. (1997), in their study of ciril bunting breeding performance and chick diet, suggested that weaker chicks begged more as a result of starvation and increased the likelihood of predation. Redondo & Castro (1992) also concluded that begging increases the risk of predation in nestling magpies. Secondly, lower growth rates could indicate chicks were not being provisioned adequately, which could be a result of invertebrate availability, weather conditions and indeed parental experience or condition.

Effects of diet composition on growth rates

Insect larvae, in the current study, were found to have a weak non-significant positive relationship with growth rates. Nestling growth rates were negatively correlated with the amount of araneae in the diet. Considering that this invertebrate group was found in a high proportion of broods' diet and the group was selected far more than would be expected, this is an unexpected result. Skylarks could have been feeding araneae to nestlings when there were no other available prey items of suitable size. When there were, chicks could have fared better. Donald et al. (2001d) found that skylark chicks whose diet included insect larvae had significantly higher body condition indices than chicks not fed larvae but no other food type had a significant effect on body condition. No effects of diet composition were found in the current study to affect yellowhammer chick growth rates although this result was anticipated because the sample size was small.

Song thrush nestling weight or tarsus growth rates were also unrelated to the diet composition of nestling song thrushes, as found by Gruar et al. (2003). A study by Konarzewski et al. (1996) on captive song thrush nestlings showed that food restriction on nestling song thrushes did not affect tarsus length, but did affect body mass. Konarzewski et al. (1996) found that nestlings were unable to actively respond to changing food availability by either increasing or decreasing their growth so concluded that growth rates in the wild are more likely to be limited by physiological or anatomical constraints rather than food availability. Tarsus is therefore less likely to show changes due to other factors than weight.

Other variables affecting nestling growth rates

The date of the start of incubation showed a weak negative correlation with song thrush chick weight gain (g/day). This weak correlation could be due to a seasonal decline in either food availability or pair breeding performance. Of the three study species, the song thrush had the longest breeding season, stretching from March to August. Song thrush pairs at Loddington were known to have between 1 - 5 nesting attempts per season, with a maximum of 3 successful broods (unpublished data). This study did not, however, investigate differences in nestling growth rates between first and last broods. Perhaps further data collection and additional analysis might identify factor(s) that drive this apparent seasonal decline in song thrush chick growth rates at Loddington.

Brood and clutch size

The apparent pattern of tarsus growth rate in response to clutch size could be attributed to the limited number of two egg clutches. Another possibility is that two egg clutches may be laid by birds in poorer breeding condition than those that lay three or four egg clutches and this is subsequently reflected in the lower chick growth rates relative to three and four egg clutches. The decline in tarsus growth rate between clutch sizes of three to four eggs may be attributed to the extra food requirements that a brood of four chicks would need to develop at the same rate as a brood of three. Testing this hypothesis was beyond the scope of this study. Donald et al. (2001d) and Weibel (1999) found that large skylark broods tended to have higher growth rates than smaller ones, as did Evans et al. (1997) for curl bunting chicks. Magrath (1991) suggested that blackbird nestling weight and not brood size influences juvenile survival.

5.5.4 Sampling methods and limitations

Results presented in this chapter are based on the assumption that the sampling methods used for measuring either invertebrate availability or chick diet were an adequate measure of what was available to the birds and what they actually took.

5.5.4.1 Neck ligature versus faecal sampling in the field

Numerous neck ligatures were put on chicks over the course of the three-year study period but many of these failed to collect data on chick diet, despite parent birds actively taking food back to the nest. This could be due to the neck ligatures affecting either the chick's behaviour or parent bird's behaviour. To minimise the effect on the parent birds, the ligatures were made from embroidery thread mimicking chick skin colour. Neck ligatures were not visually obvious on chicks, but adult birds could be gathering more subtle information on the behaviour of their nestlings despite their begging.

Johnson et al. (1980) found that in a study of gray catbirds (*Dumetella carolinensis*) adults sometimes put food into the throat of a chick with a neck ligature and then removed it, or removed food from a chick's throat if the item could still be seen when the chick begged. This may certainly have been the case with song thrush chicks since worm segments were either seen in the chick's throat before removal or occasionally found stuck to the nestling's body. Because it was difficult to obtain good throat samples from song thrush chicks, faecal samples were collected and analysed. However, unlike the skylark and yellowhammer, song thrush chicks did not defaecate each time they were handled.

Poulsen & Aebischer (1995) found no detectable difference in diet composition between nestling skylark faecal and neck ligature samples so it is probable that there may have been no detectable difference between the different samples in this study. Faecal sampling is, on the whole, a less invasive method of examining diet and has been frequently used in other farmland bird studies (grey partridge - Green et al., 1987; skylark - Green, 1978, 1980; Elemegaard et al., 1999; Donald et al., 2001a; corn bunting - Brickle & Harper, 1999; song thrush - Gruar et al., 2003; cirl bunting - Evans et al., 1997; yellowhammer - Stoate et al., 1998; Moreby & Stoate, 2000; MacCleod, 2001), whereas neck ligatures are less well used (see Moreby & Stoate, 2000). For this thesis, the main benefit of the use of neck ligatures was that it enabled easier identification of prey items than faecal samples, less skill being required to identify prey items to species level. Rosenberg & Cooper (1990) list the advantages and disadvantages of several methods used to gather avian diet samples.

Johnson et al. (1980) concluded that sampling with neck ligatures over any time interval does not accurately portray the diet since food is often disgorged from ligatured chicks. They also state, however, that neck ligatures did not appreciably affect diet composition. It was difficult to determine how long to leave neck ligatures on, since delivery rates changed per pair and were likely to be affected by environmental factors and time of day etc. All disgorged food items found in the nest from each brood were collected in this study and it is believed that they provided a good estimate of the diet composition of both skylark and yellowhammer.

The use of neck ligatures also gave an insight into the manipulation of prey items by these species, similar to studies by Ponz et al. (1999) on the diet of nestling magpies, Barba et al. (1996) on the preparation of prey by provisioning great tits (*Parus major*), Banbura et al. (1999) on the food handling time of blue tit (*Parus caeruleus*) chicks and Poulsen & Aebischer (1995) on skylark chicks. The larger carabid beetles had their mandibles and sometimes the elytra broken off. Presumably this was to protect the nestling from being bitten and to ease handling by the adult bird. Earthworms were also broken into segments to be fed to chicks. It is not known whether the adult birds fed each chick in a brood or just some of the brood due to the poor sampling results. What is clear is that provisioning adults must make choices when selecting certain chick food invertebrate prey. Prey abundance, availability and accessibility, handling time and nutritional value might be expected to determine what chicks are fed. The most frequently found prey items in the diet might not necessarily be the optimal chick food, but they may be easier for adults to find, catch and feed to their young.

The fact that the use of neck ligatures did not always produce samples was a disadvantage over faecal sampling, since more time and effort was invested in the field collecting data for diet using this method. Generally, faecal samples were produced upon handling chicks and collection was no more invasive than that. In contrast to finding no food items after sampling from a whole brood, all three species were, at some time, seen to exhibit disgorgement of prey items fed to them. This could have been because the delivery rate by the parents was so frequent or the sampling time too long (Orians, 1966) and the throats of nestlings were not large enough to hold many prey items. Not every chick in the brood would necessarily be successful in securing food from the adults in the short time that the ligatures were in place. Chicks certainly begged when they were removed from the nest, whether they had food in their throats or not. Depending on the objective of

the diet study and the skill of the researchers, the decision to use either neck ligatures or faecal sampling must be given considerable consideration.

5.5.4.2 D-vacuum suction sampling

One of the potential limitations of D-vacuum suction sampling (for the purpose of this chapter) could be a bias in the sampling of different invertebrate groups based around their morphology and ecology. Beetles hide in cracks in the ground and under stones, out of the suction range. Other larger species may not be sucked up and may well be under represented in samples. Spiders and fast moving insects can also run or fly away and some species are able to hold on to vegetation better than others, preventing their capture. Although the D-vacuum sampling efficiency can vary according to vegetation height, density and environmental conditions, (Ausden, 1996) it is very effective at sampling a wide range of taxa in different structural habitats (Thomas & Marshall, 1999). This study tried to gain a measure of invertebrate availability and abundance at different sites near to the time provisioning birds were foraging. D-vacuum sampling was considered to be the optimum sampling method for that time frame. For example 60% of carabids are nocturnal (Lövei & Sunderland, 1996), so are unavailable to the provisioning study species, and therefore do not affect prey availability at the time of provisioning nestlings. Pitfall traps, which are useful for sampling nocturnal insects and particularly beetles, were considered to be unsuitable. Sweep net sampling is a method used to sample invertebrates on vegetation (Ausden, 1996). It was not used in the current study because skylarks were always observed foraging on the ground. Yellowhammers were seen foraging perched on the crop, probably more generally for ripening grain. D-vacuum sampling could only take place in dry weather conditions so that invertebrates did not stick to the vegetation or the net, getting damaged on removal. Wet weather occasionally hindered invertebrate collection resulting in some missing data per nest.

Samples taken generally contained many of the very small, lighter species such as numerous parasitic wasps or flies. Although present and available to provisioning skylark and yellowhammer they were not considered an important constituent of nestling diet and hence not taken by provisioning adults. The D-vacuum suction sampler cannot pick up larvae or pupae that are in the ground. This may account for the result of larvae or pupae being taken by skylark and yellowhammer relatively more than expected from their availability.

However, from neck ligature samples, larvae were found in high numbers of broods and formed a large part of the nestling diet so could not be excluded from the analysis.

5.5.5 Conclusions

More conclusive results on chick diet and invertebrate availability would be achieved with a combination of sampling methods such as D-vacuum suction sampling, sweep netting, pitfall trapping and soil cores in order to gain an overall view of availability to these three study species. Comparisons of chick diet between this study's results and others could be hampered by the different sampling techniques used in each study. They may create different biases in the estimation of diet composition.

Loddington, managed for wild game, clearly aims to provide beneficial habitats that in the summer months provide an abundance of invertebrates used by a wide variety of bird species as chick food (Boatman et al., 1999; Boatman et al., 2000). These habitats, potentially rich with invertebrates, within cropped and non-cropped areas, include set-aside strips sown with kale or cereal mixes, beetle banks, field margins and grass banks and conservation headlands. Few arable farms implement such management techniques so results from this study on chick diet and growth may not be comparable with studies carried out on other farmland. When skylarks and yellowhammers fed ripening grain to their nestlings it may have been their trade off between searching for and supplying food. If grain is a sub-optimal nestling food, as suggested for corn bunting by Watson (1992), it could mean that, although habitats in place at Loddington are likely to increase invertebrate abundance, invertebrate prey items may not be accessible to birds (hence why chicks were fed grain), possibly because of vegetation structure.

Each study species was shown to select invertebrate groups to feed their nestlings non-randomly. Diet was shown to be consistent throughout the chicks' growing period. Habitat management, further targeted at increasing insect larvae, coleoptera, araneae and tipulidae by the provision of unmanaged grassy areas and set-aside mixes such as the Wild Bird Cover etc, will benefit breeding skylark and yellowhammer, as well as others such as curl and corn buntings. In terms of chick food availability and abundance, correct positioning of

favourable habitats around the farm will be advantageous to many breeding territories, rather than a few, and will probably help increase local bird populations.

For song thrushes, foraging grounds that hold good numbers of accessible earthworms close to important nesting habitats are likely to be central in maximising chick growth and brood survival. Management of ditches, hedgerows and woodlands will be vital in achieving this. On farmland, the use of selective insecticides to control not only pest species such as aphids, but also snails and slugs, are likely to benefit song thrush populations. The use of selective pesticides is recommended when pest species reach a certain threshold level but not before.

CHAPTER 6

SURVIVAL AND HABITAT USE OF FLEDGED SKYLARK CHICKS

6.1 Summary

1. The aim of this study was to develop a methodology that would allow an investigation of post-fledging skylark habitat use.
2. The period between leaving the nest (fledging) and reaching independence is one of the least well-studied aspects of the skylark's life cycle, despite it potentially being one of the most critical periods. Radio-telemetry was employed as a tool to locate individual fledglings on a daily basis to monitor survival, movement from the nest, habitat use and identify cause of death.
3. A harness was designed to fit skylark chicks about to leave the nest. One chick per brood, from 14 nests, was tagged prior to fledging.
4. A higher level of tag failure was experienced than was expected in the pilot study, despite radio-tags being professionally made.
5. Fledgling independence is likely to be achieved between 18 - 20 days for skylarks but mortality was highest in the first week out of the nest when fledglings were most likely to be dependent on parents. The fate of most tagged skylark fledglings was generally known when they reached 14 - days old, and most tagged chicks were predated whilst flightless on the ground.
6. There was a low rate of post-fledging survival, when recording unknown fates as failures, although sample size was small and further study is recommended.
7. Skylark fledglings travelled remarkably similar distances from the nest with age between years and distance travelled from the nest increased with age.
8. This short study did not achieve the aim of measuring habitat use by post-fledglings in any scientific manner. Empirical data on post-fledging survival is needed to help fill the gap in our knowledge between the time of leaving the nest and entering the breeding population the following year.

6.2 Introduction

One of the most difficult periods of carrying out research on avian species is during the period between leaving the nest and reaching independence (Sullivan, 1989; Weatherhead & McRae, 1990; Baker et al., 1995). As a result very few studies are carried out on the immediate post-fledging stage, despite parental care post-fledging usually being as long as the nestling period. Indeed, much of the research carried out on skylark chicks has concentrated on the time they are in the nest. Most aspects affecting the skylark life cycle have been studied (e.g. diet, growth and body condition) as part of many field studies throughout Europe (e.g. Schläpfer, 1988; Jenny, 1990a; Poulsen, 1996; Odderskaer et al., 1997; Donald, 1999; Weibel, 1999). Reasons for this are obvious. Once the nest has been located, it is easy to visit and carry out observations and manipulations. However, very little work has been conducted on skylark chicks once they have left the nest since they are very difficult to see and follow. Post-fledgling survival rates may be an important factor contributing to the national decline of this species (Siriwardena et al., 2000a).

Skylark chicks generally leave the nest early at around 8 - 10 days old. They are flightless and still dependent on their parents for food (Cramp, 1988). Donald (2004) reports that the whole brood leaves the nest together with the encouragement of the female parent who has a contact call reserved exclusively for this. Most studies consider skylark chicks to have fledged once they leave the nest but do not estimate how many chicks actually survive to reach independence at the age of around 18 - 20 days old – i.e. post-fledging survival. This is a large and important gap in the knowledge of this species, particularly considering the national and international decline.

For skylarks, a ground nesting passerine, leaving the nest at such an early age may be an anti-predator device. As chicks get older and more cramped in the nest they become more vocal when competing for food and therefore may attract the attention of predators. By leaving the nest before the brood is fully developed, it stands a greater chance of avoiding being destroyed as a whole. At least one chick may survive if the brood splits up. Parent birds, however, may have a more difficult task in finding and feeding individual fledglings, following their move away from the nest.

The period in which any bird species leaves the nest and becomes independent is fraught with pressures such as predation and food limitation (O'Connor, 1984; Newton, 1998). Newly fledged chicks of any species are inexperienced at predator avoidance and, indeed, most are generally uncoordinated and lack muscle development to either fly properly or move long distances. Instead, instinctive behaviours such as freezing are adopted. New fledglings are also unable to forage for themselves, so must remain in contact with adult birds in order to learn from them. This may be difficult if the brood splits up. For skylarks, it has been suggested that at least half of the fledglings in a brood will reach independence, based on observations of parental foraging behaviour on Swiss farmland (Jenny, 1990c).

Little is known about skylark chick post-fledging behaviour up to reaching independence, i.e. foraging with no reliance on their parents. Only one study has been published on skylark chick dispersal (Poulsen et al., 1998), but this study only followed chicks up to four days post-fledging. Another unpublished study was carried out in Finland to investigate the direct effects of dimethoate spray, an insecticide, on skylark chicks in farmland (unpublished data, Phil Prosser, CSL). Prosser's study involved radio-tagging chicks in the nest and using the tags to locate and catch them daily once they had fledged so that blood samples and measurements could be taken. Tags were removed when it became apparent from the fledgling's behaviour that they would soon be able to fly. These tags were fitted with tilt switches that enabled all the movements of the chicks to be recorded. As a result, their dispersal was accurately tracked and recorded from the nest. No evidence of the direct effect of dimethoate on the chicks was subsequently discovered, although sample size was small.

For most passerines, recently fledged young are notoriously difficult to locate, let alone to follow (Weatherhead & McRae, 1990; Vega-Rivera et al., 2000). Relatively few studies have taken place regarding passerine post-fledging survival (e.g. yellow-eyed juncos (*Junco phaeotus*) – Sullivan (1989), song thrush and blackbirds (*Turdus merula*) – Hill (1998), wood thrushes (*Hylocichla mustelina*) – Anders et al., (1997); Vega-Rivera et al., (2000) and lark buntings (*Calamospiza melanocorys*) – Adams et al., (2001)). Consequently there is little information on this critical period of the fledgling's life, particularly regarding movement, dispersal and survival. For the skylark, colour ringing studies and mark and re-capture studies are not often applicable.

Thomson et al. (1999) used 16 years of national ringing and recovery data to estimate song thrush post-fledging survival rates by combining information on birds ringed as nestlings with those ringed as full-grown independent first-year or adult birds. They concluded that the song thrush population decline was not likely to be driven by a decline in post-fledging survival rates (and defined the post-fledging period as 63 days following ringing in the nest), despite low survival rates. However, for species such as the skylark, which are infrequently ringed in the nest, re-sighted or re-trapped after fledging (unless as part of a study; see Delius, 1965; Wolfenden & Peach, 2001), this technique would not provide a reliable estimate of this species post-fledging survival. Both studies follow colour-ringed skylark populations in coastal dune habitats and examine survival rates but the latter is the only long-term study in the UK (19 - years) and records an overall decline in recruitment from the early 1980's to late 1990's. Wolfenden & Peach (2001) do not specifically investigate the post-fledging period.

Hill (1998) took a more direct approach in investigating post-nestling survival and intensively followed song thrush chicks leaving the nest with the aid of radio-telemetry. He found that song thrush post-nestling mortality accounted for most of the first year mortality. Anders et al. (1997) also used radio-telemetry to monitor post-fledging wood thrushes in Ozark, S. Missouri and found that the productivity of this population was affected by post-fledging mortality. Similarly, Adams et al. (2001) tagged up to 4 nestlings in each of 9 lark bunting broods in Colorado and found that juvenile buntings were subject to high rates of post-fledging mortality. Low post-fledging survival could therefore affect the number of first-year birds available to enter the breeding population.

Other passerine studies on post-fledgling survival (e.g. fledgling house sparrows (*Passer domesticus*) - Pers. comm. Kate Vincent; American robins (*Turdus migratorius*) – Weatherhead & McRae, 1990; song thrush - Thomson & Cotton, 2000), adopted a method of intensively searching the area around a nest a week or so after fledging, starting at the nest and moving away in concentric circles. This technique was not considered suitable for skylarks since they are extremely cryptic and are most often found in dense vegetation and crops, without being able to fly very well.

The aim of this chapter was to (i) develop and test a radio-tag harness to fit skylark nestlings and post-fledglings and (ii) to investigate skylark post-fledging habitat use, movement from the nest and survival using radio-telemetry as the monitoring tool.

6.3 Methodology

In order to investigate skylark habitat use post-fledging it was important to have reliable means to be able to follow them. Unlike the adult birds, which are highly conspicuous when flying, singing or provisioning young, newly fledged skylark chicks are small, highly cryptic and flightless. Radio-tagging was deemed the only suitable technique for reliably monitoring their movements and survival.

6.3.1 Development of a harness

In order to use radio-telemetry as the monitoring technique, a suitable means of tagging small chicks in the nest had to be established. Since the chicks were still growing, attachment of radio-tags by glue on the back was dismissed because of the damage that would be caused to the new skin and developing feathers. Tags were required to remain attached to the chick for, ideally, over 15 days. Chicks had very little tail feather growth so attachment here was also not an option. As a result, a harness design, adapted from the one used in the song thrush study (for the design see Hill, 1998; Hill et al., 1999a), was made to loop around the chick's thighs for the tag itself to sit on the synsacrum (see Rappole, 1991). Handling and tagging of the chicks may have affected their survival (White and Garrot, 1990) although it was beyond the scope of this project to investigate this. However, extreme care was given to the welfare of the chicks at all times, and permission to carry out this work first had to be granted by the BTO Licensing department. In 2001 permission was granted to attach 12 tags, and a further 15 in 2002.

6.3.2 Materials

Pickled 7 - 8 day old skylark chicks that had died before fledging in 2000 were used to measure and fit the loop lengths and elasticity of the cord for the harness. The adapted song thrush back-pack harness design was

tried on the dead chicks, but the position and angle of their wings is very different to that of a song thrush and resulted in restriction of their wings. The alternative was to fit the loops around the legs.

The harness was made from a length of thin woven polypropylene cord, from which the free central string was removed with tweezers and replaced with sheering elastic (absolute stretch limit for each loop on the skylark tag was 450mm). This elasticised cord length was attached in the centre to the top of the radio-tag with superglue. A single thickness of cotton thread (double thickness used in the song thrush harness) was passed up through the centre of a narrow plastic tube attached to the bottom of the tag and passed around one end of the harness loop, back along the length of the tube and back through the centre, firmly attaching the free ends of the bathroom cord to the plastic tube to form the harness loops. A single knot was tied in the cotton thread (a double knot dabbed with superglue in the song thrush harness), which meant that the cotton was likely to erode faster and break. When the cotton broke, both sides of the harness loops would be released at the same time. This formed the harness's weak-link and ensured that it completely fell off the chick. Plate 1, in Chapter 6 Appendix, shows a skylark nestling of 7 days old fitted with the harness.

The woven cord provided a soft buffer across the thigh skin to minimise chafing, and the elasticity in the cord ensured restricted stretch when the bird grew and moved. The top of the tag, over the cord, was covered in potting solution (a liquid black plastic that hardened on contact with air) to provide extra protection and waterproofing. The harnessed tags were specifically designed so that one person could fit them, minimising the stress to the bird. If the weak-link broke and the tag was still transmitting, it could be recovered for examination to help determine the cause of death. The weak-link did not ensure that the tag would fall off if a chick got tangled in vegetation since the chicks body weight would not be enough to cause it to snap. The weak-link would only break due to mechanical wear and deterioration over time. The length of time the tag would remain on the bird was not tested but all precautions to ensure that the weak-link would deteriorate as quickly as possible were made.

The 0.6g PIP21 single button celled radio-transmitters, with thermistors, were made and supplied by Biotrack, (52 Furzebrook, Wareham, South Dorset), and weighed less than the recommended 4% of the body weight

(White & Garrot, 1990; Kenward, 2001). Tags had a range of over 200m metres across flat terrain. The author made and fitted the harnesses.

6.3.3 Radio-tagging and tracking

On day 6, all chicks in the brood were weighed and measured. They were then ringed with both a BTO metal ring and an individual colour-code comprising a single year code on one leg and a unique double ringed colour code on the other tarsus. Tag life was considered to be around 10 - 15 days. To maximise tag life during the post-fledging period and to prevent premature fledging, a tag was fitted to one chick in a brood on day 7. One chick per brood was selected to maintain independent samples. Handling time during harness fitting was minimised by the ringing all the chicks in a brood the day before. All chicks, except the smallest, were put in a cotton bag and one was randomly picked out and fitted with the harness. All chicks were placed back into the nest together. Ideally chicks were over 18g when the tag was fitted and many were over 20g.

The radio receiver was used from the day of tagging to find out exactly when chicks left the nest and if they survived. This was backed up with a visual sighting, ensuring minimal disturbance approaching the nest. Once the chicks had fledged, a fix was taken three times a day, at different times (including checking the fledgling's position at dusk and dawn), in the same manner that song thrush fixes were taken in Chapter 3. After the fix was completed, the fledgling was then located with the use of the receiver to check the harness fitting. It could take several minutes to find a fledgling, despite being extremely close to it, because it was so well camouflaged. Care had to be taken on moving vegetation aside before placing a foot down. Notes on the welfare of the fledgling, the harness fit, behavioural observations, whether any siblings were around and the habitat type were made. The location was recorded using a hand-held GPS. Fixes plotted on to maps (using methods described in Chapter 3) were compared to GPS readings and distance from the nest and the last recorded place was calculated. The addition of thermistors to the transmitters enabled data on mortality to be recorded and for tags to be recovered from dead birds. It was hoped that this would enable the cause of death to be identified.

6.3.4 Post-fledging survival estimates

Using methods described in Chapter 2, section 2.3.4.3, daily survival estimates of skylark post-fledging were calculated using an estimated 11 - day period to reach independence from fledging.

6.4 Results

Unfortunately, despite intensive efforts to tag and monitor as many fledglings as possible, this project was hindered by tag failure, predation of broods before reaching fledgling age and the lack of nests in 2002. Results in this chapter are therefore mainly descriptive, since statistical analysis was not possible due to limited sample size. 14 skylark chicks were tagged, 6 in 2001 and 8 in 2002.

6.4.1 General behaviour of skylark chicks in the nest

Hatching weight, at day 0, of skylark chicks was approximately 3.37g ($n = 3$ broods). Chicks were almost naked, blind and helpless, had little co-ordination and were unable to thermoregulate. They were continually brooded. Newly hatched chicks lifted their heads to beg when high pitched noises were made (by the author to aid their location), but they were generally silent. By day 3, their eyes were almost completely open and they begged instinctively when the nest was approached or when a high-pitched noise was made. There appeared to be no predator recognition. Feather development had started and the soft downy feathers covering the head and body had begun to be replaced with feathers 'in pin'. Chicks were left for longer periods of time in the nest so presumably could self thermoregulate. Wing feather development could also be seen. By day 5, chicks were aware of possible predators and when the nest was approached they would quietly flatten themselves in the nest and move away from the hand when they were being removed from the nest. Generally they would 'freeze' when being handled. On day 6 chicks were ringed. The skin on their tarsus had hardened considerably and they were almost fully feathered apart from the areas on the sides on their bodies under the wings. Primary feather development was around 3 - 5 mm out of pin. By day 8, mean chick weight was $19.59\text{g} \pm 1.63\text{g}$ and mean tarsus length was $20.98\text{mm} \pm 0.52\text{mm}$. Tarsus growth was rapid while tail

development was comparatively slow. All chicks appeared to leave the nest together. No nest was found with a partially fledged brood.

6.4.2 Post-fledging

The average age that chicks left the nest was $9.5 \text{ days} \pm 0.20$ (range 8 - 12, $n = 32$ broods). The average age of chicks, fitted with a harness, that successfully left the nest was 9.89 ± 0.46 , (range 8 - 12, $n = 9$). As harnesses were fitted to one chick in each available brood at day 7, tags were active for between 1 - 5 days before they left the nest. With tag life only extending for approximately 10 days, this severely reduced the chances of gathering good post-fledging data. Maximum tag life recorded was 16 days. This particular chick was predated at this point. When the signal stopped from the tags, it could have been because the battery died, or the tagged chick was removed from the area by a predator, or the chick reached independence and moved on. It was sometimes difficult to determine accurately the exact outcome and individual assessment of the situation had to be made, for example taking the age of the fledgling into account.

6.4.3 Harness fitting

Mean weight of chicks when fitted with a harness was $22.7\text{g}, \pm 0.87$ ($n = 14$). Each chick fitted with a tag was checked daily. Any signs of skin damage, bleeding, rupturing and restrictions were looked for. One chick (out of 14) still in the nest experienced chafing around the top of the thighs. The harness caused weeping, but the skin was not broken and there was no bleeding. Once the chick had left the nest this dried up and healed quickly so the harness was left on. Movement in the nest was restricted as chicks got larger, and it was considered, by the author, that the tightness of space did not allow the harness to fall in to its natural place until the chick left the nest. When chicks were older and were moving around more, tags that lay across the spine sometimes rubbed to form a callous. Feather development under the tag was damaged and was similar to that observed with the song thrush harness.

6.4.4 Behaviour and movements of tagged fledglings – changes in responses with age

Once chicks fledged they were located using the hand-held receiver. Immediately after fledging, fledglings travelled a short distance from the nest (mean = $27.73\text{m} \pm 7.047\text{m}$, range = 9 - 72m, $n = 9$). They were highly cryptic and this coupled with their 'freezing behaviour' on approach, often made it extremely difficult to see them, despite knowing their precise location. Fledglings tended to be found in areas that were not thickly vegetated (e.g. next to tramline edges rather than within the crop). Small piles of faeces often surrounded the chicks, indicating their location. This suggested that in the early days following fledging they remained in the same place for a considerable amount of time, probably waiting for adult birds to bring in food. Indeed, a parent bird often flew out alarming from an area close to where the fledgling was located, suggesting that parental care was quite intense to begin with. Fledglings were located at dusk and again at dawn the following day at least once when they were tagged to see whether they moved during the night. They were generally found in the same place suggesting that they did not move overnight.

As fledglings got older they moved further from the nest (average distance travelled per fledgling = $20.78 - 138.57\text{m}$, $n = 9$). The average maximum distance fledglings travelled from the nest was $137.49\text{m} \pm 30.75$ and the average overall distance travelled was $69.10\text{m} \pm 13.52$. The overall average distance fledglings travelled between fix places was $37.95\text{m} \pm 5.17$, $n = 9$ (see Table 1 for details). There was no significant difference in the distance travelled by fledglings in 2001 and 2002. Figure 1 shows that chick mobility in the two years was remarkably similar and increased with age ($F_{(1,13)} = 8.391$, $P = 0.012$, $R^2 = 0.392$). Neither year nor chick age affected distance travelled between fixes on consecutive days, although distance from the nest increased with age ($F_{(9,14)} = 2.747$, $P = 0.066$, $R^2 = 0.810$).

There did not appear to be any consistent direction in which fledglings travelled, except that they generally followed a habitat feature, (e.g. along a tramline, along set-aside edges), but data were scant and not conclusive. Only two fledged chicks moved between habitat types. All the others remained within the habitat type that the nest was in. Chicks no longer froze when approached and would often move away. If handled, they were vocal and struggled in the hand. When replaced on the ground they would run a short distance into the vegetation before stopping (rather than freezing as before).

Table 1: Outcome of radio-tagged skylark chicks in 2001 – 2002. Table includes details of number of fixes taken, distances travelled by the chicks and outcome. Habitat type refers to the habitat type the nest was in; W.Beans = winter beans, KSA = kale set-aside, P.SA = permanent set-aside, WW = winter wheat and WB = winter barley.

Chick #	Year	Habitat type	Chick weight when tagged		Age tagged	Age fledged	# days tagged b/f		# fix days	# fixes	Tag life	Outcome	Chick age on Outcome	# different habitats used	Max. dist from nest (m)		Av. Dist from nest (m)		Av. b/w fixes (m)
			g	g			fledge	fledge											
1	2001	W.Beans	24.7	7	7	11	4	4	12	19	13	Successful	19	1	228.99	70.80	45.92		
2	2001	KSA	22.6	8	8	12	4	5	12	12	10	Unknown	18	2	120.29	67.74	32.67		
3	2001	Track	26.3	7	7	9	2	0	0	0	1	Unknown	9	-					
4	2001	Verge	17.1	7	7	9	-	-	0	0	2	Predated	9	-					
5	2001	P.SA	20.3	7	7	8	1	3	7	7	3	Unk/Prod	10	1	40.00	20.78	28.03		
6	2001	KSA	23.5	7	7	10	3	4	6	6	8	Unknown	15	2	291.17	138.57	37.00		
7	2002	WW	-	7	7	-	-	-	0	0	-	Died	11	-					
8	2002	WW	-	7	7	11	4	8	11	11	13	Unknown	18	1	232.00	126.92	55.20		
9	2002	WW	18.8	7	7	10	3	14	22	22	16	Predated	23	1	106.00	71.82	24.13		
10	2002	WW	22.4	7	7	-	-	-	0	0	-	Predated	10	-					
11	2002	WW	21.9	7	7	-	-	-	0	0	-	Predated	11	-					
12	2002	WB	27.0	7	7	10	3-4	10	15	15	14	Unknown	21-22	1	113.00	56.73	51.07		
13	2002	WB	26.0	7	7	11	4	7	17	17	8	Unknown	17	1	80.00	43.80	56.50		
14	2002	WB	21.7	7	7	8	1	1	4	4	-	Died	9	1	26.00	24.75	11.00		

Notes on chick outcome:

- 1: Tag battery died. Bird seen alive and flying
- 2: Tag battery died.
- 3: Tag found complete and undamaged in the 1st year cereal strip about 4m from the nest. Reason unknown.
- 4: Predated just outside the nest as the chicks were fledging. Tag re-used.
- 5: No signal 1 hour after taking a fix. Kestrel predation thought to be a possibility.
- 6: Tag battery presumed to have died (it was a recycled tag). 31/7/01 – no signal. Chick followed edge of set-aside on leaving the nest.
- 7: Fledged and died about 1m from nest 21/5/02. Reason unknown.
- 8: Tag stopped on 7/6/02 – never located.
- 9: Predated 11/6/02, in a fox den. 23 days old – could have been independent
- 10: Predated aged 10 next to nest, feathers all around, 30/5/02. May have just been fledging.
- 11: Predated about 2m from nest. May have just fledged on the 31/5/02. Brood predated.
- 12: Tag signal stopped on 17/6/02. Unknown reason.
- 13: Tag signal stopped on 23/7/02. Unknown reason, possibly predated.
- 14: Died on 31/7/02, rain and no shelter from sun. Plagued by flies.

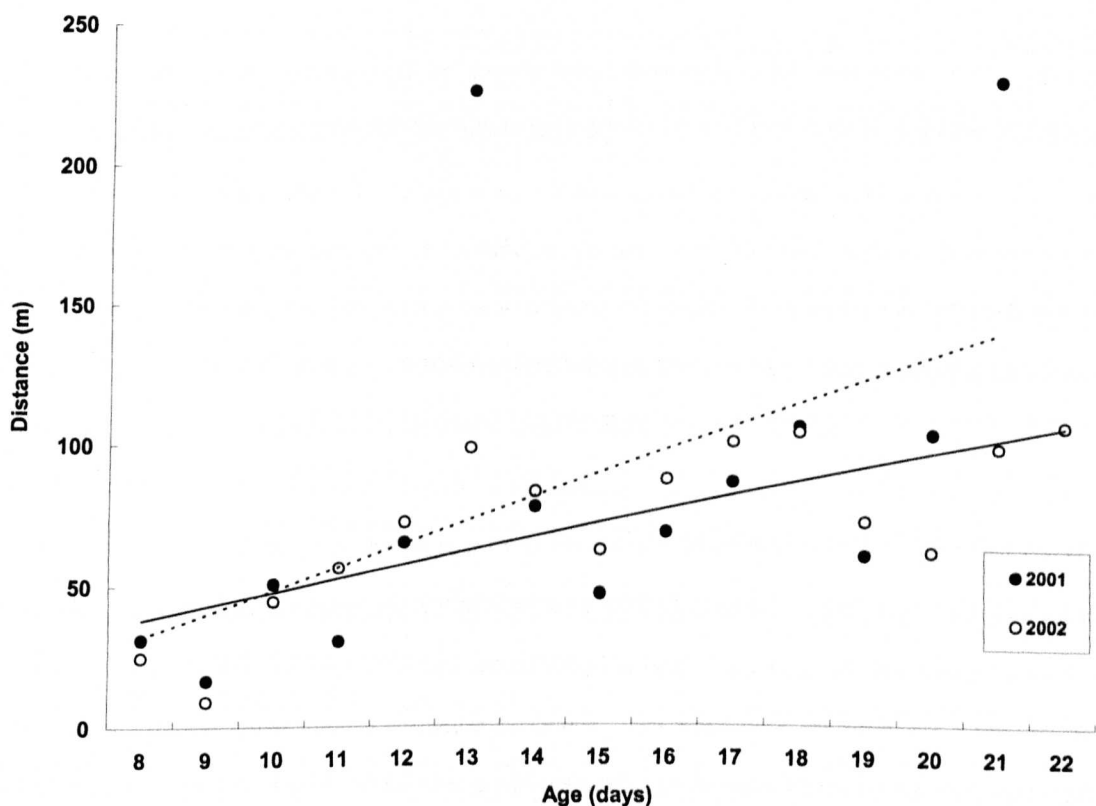


Figure 1: Distance travelled (m) away from the nest by radio-tagged post-fledged skylark chicks with age. 2001, $y = 8.209x + 23.869$, $R^2 = 0.275$ and 2002, $y = 4.83x + 33.234$, $R^2 = 0.541$.

6.4.5 Battery failure

Problems were experienced with battery life in 2001, which resulted in all tags being returned to the manufacturer to be re-charged. Chicks remained in the nest for an average of $2.9 \text{ days} \pm 0.38$, (range 1-4 days, $n = 10$) after being equipped with the tag. Battery life was otherwise on average $7.88 \text{ days} \pm 1.38$ (median = 7, range 3 – 14, $n = 8$) once the chicks left the nest. This meant that it was often inconclusive when tags lost their signal, whether it was due to birds fledging properly (estimated to be around 18-20 days), to tag failure or battery life exhaustion or due to the chick being carried away from the area by a predator. Only 3 chicks were followed for 10 days or longer, and with tag life being just over 10-days on average, including the time period spent in the nest, it proved difficult to follow chicks to independence with the radio-tag used in this project.

6.4.6 Outcome and tag recovery

Table 1 details the outcome of tagged chicks. Results from this study highlight how difficult it is to determine the exact outcome once chicks have left the nest around day 8 - 9. Out of 14 chicks tagged in the nest, only one was known to fledge properly (7.14%) and it flew away when approached at 19 days old. Five tagged chicks (35.71%) were predated as they were fledging, at the ages of 9 - 11 days. Of these, three whole broods were predated and their remains were found next to or close to the nest. From another brood, the harness of a chick was found intact, with no tears, visible over-stretching or blood on it. It was concluded the chick was most likely to have been predated, but it remains unclear by what.

The average age of fledglings when the outcome was known was $14.29 \text{ days} \pm 1.33$ (range = 9-23, $n = 14$). This is below the age when independence is estimated to be reached, (generally 18-21 days). Overall, the best-case scenario was 42.86% of tagged chicks successfully fledged (including all successful and unknown outcomes) and 57.14% failed (due to predation or dying). The worst-case scenario was 7.14% of chicks leaving the nest at 8 days old survived (all successful outcomes) whilst 92.86% died either through predation at fledging or otherwise (all unknown and predated outcomes). Over half the tagged chicks that fledged died in the first week (55.55%). The daily survival rate after fledging was calculated as 0.817 ± 0.050 when recording nests with 'unknown' outcomes as failing and as 0.917 ± 0.036 when recording nests with 'unknown' outcomes as successes. The probability of a skylark fledgling surviving for 11 days after leaving the nest was at worst case 0.108 or at best case 0.384.

42.8% of tags stopped transmitting, for chick numbers 2, 5, 6, 8, 12 and 13, either due to battery life exhaustion, predation, or genuine fledging (Table 1). Observation suggests it was possible for chicks 2, 8 and 12 to have reached independence but that chicks 5, 6 and 13 were most likely to have been predated, being less than 18 days old. Chick 5 fledged in a block of permanent set-aside with mature woods on either side. Kestrels (*Falco tinnunculus*) were frequently seen hunting over that area and it is possible they could have taken the chick.

One fledgling died (7.14%) from exposure to heat (chick number 14). This chick fledged from one of the last nests in the season, in winter wheat, and survived harvest. The nest was then left open and the brood was exposed to heat or rain in the day and dew in the night. The brood became fly blown very quickly and chicks left the nest at day 8 with no vegetation to hide in. A fox predated chick 9 at the age of 21 days, after it had been successfully followed for 14 days. Its tag was found down an earth 157m from the nest and 194m from its last fix position. This fledgling could fly short distances and had reached independence.

Chicks that were predated at the time of fledging were most often found next to or close to the nest with their dead siblings around them. Their bodies were sometimes partially eaten, torn apart or nibbled. Exact predators remained unknown, although weasels, foxes, sparrowhawks (*Accipiter nisus*) and kestrels were frequently seen. No tag fell off due to the weak-link breaking and no chick was ever found caught in vegetation.

6.4.7 Notable field observations

The soil at Loddington is mainly clay. Two chicks that left the nest during wet weather were often subsequently found with 'clay balls' on their feet. The clay hardened around their toes often sticking the back toe to the rest or indeed to the stomach feathers if the bird had been sitting for a long period of time. Once the clay was dry there was no possible way that the chicks could break the clay to free their toes. This could result in chicks dying from starvation or chilling and would increase the chances of predation. In this situation, however, the author removed the clay when the chicks were caught and examined.

6.5 Discussion

6.5.1 General issues

A radio-tag harness combination to fit skylark chicks was successfully made and tested in the field. However, a conclusive acceptance or rejection of the hypothesis "Newly fledged skylark chicks use habitats available to them randomly" was not possible by the end of the two-year study. Unfortunately, the first chick was

equipped with a tag in late June 2001 and the season finished in August. In the second year, the project was hindered by apparently poor breeding performance so the potential number of individual skylarks that could be tagged was low relative to the previous year.

For example, in 2001, 30 nests were found and, of these, 17 successfully fledged young, compared to 14 nests being found in 2002 with 6 fledging young. From early June onwards in 2002 very few skylark territories were mapped (unpublished data) and birds were obviously absent from areas where they had been active in the month before. Only two nests were found in June and July, compared to 8 and 10 in the previous years. It is therefore possible that the sample of chicks used to test the hypothesis was not representative of the population at Loddington. In order to test the hypothesis set out, a large number of nests is required to account for (i) subsequent nest failure and, (ii) the number of tagged individuals required. Since each chick should be an independent observation, only one chick from a brood can be selected. Fledglings are also required to survive more than a week if any measure of habitat use post-fledging is to be made, even though measures of survival post-fledging will still be gained.

6.5.2 Harness design

As happened with the song thrush harness, feathers under the tag were damaged, due to movement and friction. This did not appear to hinder the chick's movement or welfare but it should be taken into account when tags are used. No tag was found with a broken weak-link and it remains unknown how long it would take for the weak-link to deteriorate enough for the tag to fall off. This is a shortfall of the project and could warrant a study on captive-held birds if tags were to be used for skylarks in the future. Certainly for the song thrush some tags were still intact on the bird over a year after fitting, although it had been estimated they should come off after 6 – months (Hill, 1998). Callouses also formed on the inter-scapular area under tags of the song thrush, although the individuals concerned were healthy when caught and examined.

The skylark harness design was considered to fit fledged chicks well and did not appear to restrict movement. However, the behaviour of harness-wearing chicks could be impinged. For example, if the wearer was uncomfortable or movement was hindered while wearing the tag, it is quite possible that predators would have

been able to detect or catch fledged chicks on the ground more easily. If discomfort increased, as chicks got larger, then it is also possible that their begging rates were affected or their ability to start foraging themselves might have been lowered. Furthermore, if starvation had been apparent, this may not have been an effect of the harness itself since it has been suggested that not all chicks from a fledged skylark brood will be fed. Donald (2004) suggests from observation of skylark parents that they feed only a couple of chicks that fledge, since the brood splits up and disperse. There was some evidence in this study to suggest that siblings are not spatially isolated and could stay in contact with each other. On location of a tagged chick, its identity was confirmed by the presence of the tag and individual colour ring identity. Occasionally another chick was found before the tagged chick and would be in close proximity to it. Certainly from the mid-breeding season onwards, juvenile birds were often seen flying in territories of breeding adults, which could suggest that they re-unite once independence is reached. Brood division into two groups upon fledging and the coming together of chicks and parents, when fledglings approached independence, was observed by Adams et al. (2001) with lark buntings. Further study into post fledgling skylarks could help to determine if this is also the situation with this species.

The current study tried to examine chicks for any external affects of the harness. After chicks left the nest, the harness was large enough to accommodate growth and did not appear to chaff the skin. Recovered corpses were also examined externally. Even though most were the obvious result of predation, harnesses were still intact and no external damage due to the harness was clear. It was beyond the scope of this study to examine any internal effects of the harness, although these cannot be discounted.

Without a more detailed study, including a measure of examining habitat use and survival of non-tagged chicks, conclusions drawn from this study have to be treated with caution. It is unlikely that a comparison of tagged and non-tagged fledglings could be made in the field and it is doubtful if a captive study of this species during post-fledging could be made. Nonetheless, it is important to try to quantify fledgling success as far as possible and this study has provided a valuable insight into just how few fledglings could reach the age of independence.

6.5.3 Habitat use

This study found evidence that fledged skylark chicks appeared to utilise the habitat in which the nest was situated. Parent birds did not appear to lead chicks to their preferred feeding grounds (see Chapter 3). Most of the tagged chicks stayed within the habitat type that they fledged into and did not travel further than 232m from the nest, although this distance could easily incorporate a mosaic of habitats. This could suggest that, during the dependent stage, fledglings remain in their natal territories close to the nest and when independence is reached will disperse further or even leave them. Distance travelled is restricted by their own mobility, which increases with age and development.

Two tagged fledglings did move into a second habitat type. It is likely that one of them followed the edge of a habitat feature (the side of a set-aside strip) until it could move no further along, and then changed direction into a field margin parallel to a hedge, a habitat type skylarks usually avoid (Wilson et al., 1997a; Buckingham, 2001). This long distance movement by a single chick accounts for the outlier in Figure 6.1 at day 13. A parent bird often flew up close to where tagged fledglings were located. This could indicate that adults were foraging for the fledglings near to where they were situated. Poulsen (1996) suggests skylarks are 'multiple central placed foragers' when feeding fledglings since a parent spends some time foraging and feeding each fledgling separately around the area where it is settled, before locating the next fledgling and doing the same there. Foraging travel distances would be shortened, reducing the energy costs to the parent birds themselves. The current study did not have data to further investigate this. Adams et al. (2001) recorded brood division upon fledging in 67% of lark bunting broods studied. Weatherhead & McRae (1990) also recorded brood division in American robins and Vega-Rivera et al. (2000) in wood thrushes. Parental foraging efficiency may be increased using this strategy if food abundance or accessibility on a study site is limited.

As a semi-precocial ground nesting species, which is reliant on rapid tarsal development for leaving the nest, skylark post-fledging survival strategy in the dependent stage may be to leave the nest as early as possible to avoid whole brood predation, but to stay within the vicinity of the nest until independent. At what age that happens remains unknown. Poulsen's (1996) paper is the only published UK study concerning post-fledging skylark chicks, albeit with small sample sizes like this study. He studied post-fledging behaviour by observing

adult birds feeding fledglings up to four days after they left the nest, after which they were too difficult to follow. He found fledglings travelled further from the nest with increasing age, which this study supports. One of the major shortcomings of his study is the fact that he only managed to follow chicks four days after fledging and could not make an estimate of habitat use or post-fledging survival after that. Neither of these studies examined post-fledging chick diet, which could help determine dietary changes with age and possibly provide more light on habitat use and post-fledging survival.

6.5.4 Post-fledging survival

Most studies on skylarks, or indeed any bird species, record successful nests as those that fledge at least one chick. Nest success is therefore not based on survival of individuals, unlike when examining individual post-fledging success. The difference between what constitutes a successful fledging and successful post-fledging is therefore apparent and important. In this study, results showed that in 2001 and 2002 52.27% of nests ($n = 23 / 44$) successfully fledged at least one young and of these, 14 nests had chicks tagged. 64.29% of nests with tagged chicks fledged young and 7.14 – 42.86% reached independence. Most fledglings did not appear to survive longer than 14 days, almost a week away from reaching independence. The 11% probability that a fledgling could survive to reach independence appears low (although this is the most pessimistic assumption since it recorded 'unknown outcomes' as failures), while the 38% probability that a fledgling could survive to reach independence may be over optimistic (since it recorded all 'unknown outcomes' as successes). However, this is not to say that other chicks from the same brood did not reach independence and the only way to determine exactly how many survive to independence is to monitor the whole brood.

Adams et al. (2001) tagged between 1 - 4 lark bunting nestlings in a brood and found that fledglings moved up to 25m from the nest by fledging day 6 and up to 100m by fledging day 13. Three weeks post-fledging lark buntings were travelling distances of up to 800m from the nest. Hill (1998) tagged all blackbird and song thrush chicks in a brood and found that fledglings rarely moved further than 100 and 150m from their nest up to 15 days after fledging, and before reaching independence. This is a considerably shorter distance travelled than that of skylark chicks in this study, who sometimes moved over 200m 8 days after fledging. Both fledgling blackbirds and song thrushes are known to spend a lot of their time in vegetation for the first two

weeks after fledging (Hartley, 1967; Simms, 1978) and, like the skylark, are incapable of proper flight. Skylark fledglings in this study were often located in bare patches of ground or in the edge of a crop tramline. They did not obviously hide in cover, which could have increased their risk of predation. Predator control may play an important role during the breeding season and could potentially help increase post-fledging survival rates.

From the analysis conducted in Chapter 5, it is clear that the management of set-aside at Loddington is beneficial to breeding productivity, as it not only improves brood growth rate but also positively improves nest success. However, Loddington's skylark population has remained stable since management techniques were put in place in 1993. This could be due to constraints imposed on the population by changes in other key demographic parameters such as recruitment and/or survival (including post-fledging, first year or adult survival) during the same period.

6.5.5 Starvation

After chicks have left the nest, parent birds are under more pressure to feed chicks that have split from the brood. As chicks get older, they should be learning to forage and handle prey for themselves. As a result they may lose weight (Sullivan, 1989) and, in the worst case, starve. Food availability and abundance around the chicks, unless they are highly mobile, will play a part in this, as will the habitat type in which they locate. Most tagged chicks in this study fledged into cereal crops, which compared to non-cropped habitat types may hold less potential invertebrate food resources (Thomas & Marshall, 1999; Wilson et al., 1999; Vickery & Buckingham, 2001). When caught and examined, none of the tagged fledglings seemed to display obvious signs of weight loss, so it is unlikely that causes of death were primarily due to malnourishment in this study. However, if fledglings had survived longer they may have been more prone to starvation, until they could catch and handle prey efficiently, when they were no longer reliant on parents (Sullivan, 1989). The clay soils proved a difficult hurdle in wet weather for skylark fledglings, preventing them from moving freely. Factors such as this can play a role in post-fledging survival since it could account for many deaths during wet years and help explain why Loddington's skylark population has remained relatively stable since project management began. Loddington may prove to be an unsuitable site for fledgling skylarks during wet weather.

Indeed, grey partridge chicks suffered the same problem at this site and were regularly found by the resident gamekeeper incapacitated with 'clay balls' on their feet (Malcolm Brockless, pers. comm).

6.5.6 Predator control

In 2002 predator control across the farm ceased. Although this was not shown to have an effect on skylark nest survival (Chapter 2), it may have had an impact on post-fledging survival. Results showed that predators had a major impact on post-fledging survival of tagged chicks. In 2001, no predator control took place along the set-aside strips, apart from fox control, and smaller predators such as stoats and weasels were often seen running down them. Aerial predators, never controlled, such as kestrels, sparrowhawks and barn owls (*Tyto alba*) were also frequently seen hunting above set-aside and could easily take young skylark fledglings. Adams et al. (2001) found that raptors preyed on lark buntings post fledging, whereas mammals posed more of a threat during the egg and nestling stage. Anders et al. (1997) also found predation to be the largest cause of mortality of wood thrush, particularly in the first week out of the nest, as did Sullivan (1989) for yellow-eyed junco and Hill for song thrushes and blackbirds (1998).

Similar behavioural responses to being found by a 'predator' (freezing) on the first few days after fledging were also recorded by O'Connor (1984), Magrath (1991), Anders et al. (1997), Hill (1998) and Vega-Rivera et al. (2000) for various passerine species. The latter studies also found that, towards the second week post-fledging survival increased as predator avoidance behaviours developed. Post-fledging independence was likely to be reached in these studies around 4 - 5 weeks after fledging rather than around two weeks in this study. It would appear that a predator avoidance strategy develops after fledging, presumably once fledglings are able to move faster and have more co-ordination, despite still being dependent on parents for food. The rapid development of tarsal length in skylarks is believed to enable a quick 'flight response' if necessary (Donald, 1999). However, skylarks appear to behave like many other passerine species that have no apparent need for such rapid bi-pedal development. It is suggested here that rapid tarsus development is mainly to enable them to move away from the nest as quickly as possible, to avoid whole brood predation, but then remain in the vicinity of the nest to allow parent birds to find them and feed them more easily. As age increases, so do muscle and feather development, which enables them not only to avoid predators with greater

ease but also to move to feed themselves. In the current study, skylark fledglings were able to make short flights around 21 days old. Brood separation on fledging would therefore serve to protect the chicks from predation. Most fledglings, however, are predated within the first week, which is similar to other post-fledging passerine studies (e.g. wood thrushes - Anders et al., 1997, song thrush and blackbirds – Hill, 1998).

6.5.7 Conclusions

In order for the declining skylark population to increase, fledged birds must first survive to independence, then, through winter, to enter the breeding population and to successfully fledge young themselves. The critical period between leaving the nest and attaining independence is estimated to be around 8 - 10 days for skylarks, approximately the same as the nestling period. Magrath (1991) suggests that the number of young surviving to independence may be a better estimate of reproductive success than the number of young to fledge, which may often be a biased approximation. This may be true for the skylark, since mortality in the first week out of the nest at Loddington was high. However, due to poor tag performance it proved difficult to assess survival in the required detail. Therefore, in order to gain a better estimate of reproductive success, more studies encompassing the critical period of post-fledging are required. These would require careful planning to ensure an appropriate sample size and should span multiple breeding seasons to help determine the relative influence of different factors on post-fledging survival.

Appendix 6, Plate 1: A 7-day old skylark chick fitted with a radio-tag and harness.



CHAPTER 7

GENERAL DISCUSSION AND FUTURE RESEARCH RECOMMENDATIONS.

7.1 Introduction

Skylarks, yellowhammers and song thrushes have previously been the subject of single species studies on farmland (e.g. Donald, 1999; MacCleod, 2001; Peach et al., 2004), but no earlier published study has intensively studied all three simultaneously on a single site. Loddington was unusual in that it provided a study site that operated as both a working and a demonstration farm. Loddington therefore provided a study site which carried out accepted good farm practices including crop rotation, selective use of pesticides when pests exceeded a threshold level, hedgerow, ditch and woodland management and the establishment of many other non-crop habitats to benefit, primarily, wild game (see Boatman & Bence, 2000; Boatman & Stoate, 2000). Wild Bird Cover crops were developed to enhance set-aside for wild game in summer, as brood rearing cover and chick food, and in winter, as shelter. This habitat simultaneously benefited many declining passerine species and other wildlife (Boatman & Bence, 2000). The establishment of managed set-aside is, however, uncommon on farmland unless the landowner has a specific interest in game, since no further management payments are received. Nevertheless, it is the provision of managed set-aside at Loddington that makes this study unique when examining habitat use by skylarks, yellowhammers and song thrushes during the breeding season. Results reflect a single study site and it could be argued that they may not be comparable with results from other studies on the same species in different areas. However, the key findings from this thesis support much of the work carried out across the country on the same species, reinforcing the results. The findings described in this thesis, together with those of other studies, can improve beneficial management practices on farmland for skylarks, yellowhammers and song thrushes, when included as part of future agri-environment scheme developments. Currently there is a demand for dramatic changes in agricultural policy and industry to be made if conservation of these species is to be successful.

7.2 Summary of key findings

The key factors influencing foraging by breeding skylarks, yellowhammers and song thrushes at Loddington were identified as:

- *Nest site location and nest density.* The highest proportion of skylark, yellowhammer and song thrush nests were located in cereal crops and set-aside, 'other vegetation' and woodland respectively, Nest densities were highest in managed set-aside for skylarks, herbaceous vegetation and field boundaries for yellowhammers and hedgerow and woodland habitats for song thrushes.
- *Predation.* The highest cause of nest failure for skylarks, yellowhammers and song thrushes was shown to be predation.
- *Foraging habitat availability.* None of the study species foraged randomly across the farm. They utilised some habitats more than would be expected relative to their availability. Set-aside, particularly managed set-aside (cereal or other crop or kale-based mixtures), was selected by provisioning skylarks and yellowhammers and woodland and field boundaries were selected by song thrushes. Cereal crops were particularly important to provisioning skylarks and yellowhammers. Cereal crops and set-aside were habitats least used by provisioning song thrushes. Skylarks and yellowhammers used habitats near to buildings and pasture least.
- *Vegetation structure* influenced foraging patterns within winter cereals for skylarks and possibly yellowhammers. Sparser vegetation allowed greater access to bare ground, potentially enabling better manoeuvrability, visibility and quick flight responses from predators. However, vegetation density was shown not to affect the foraging of song thrushes.
- *Invertebrate availability and chick diet.* Although there was no evidence to suggest that individual species selected areas with higher invertebrate abundance within the same habitat type, skylarks, yellowhammers and song thrushes showed dietary preferences for certain invertebrate taxa at foraging sites. Skylarks foraged in areas of winter wheat with significantly more araneae than yellowhammers, although they selected very similar invertebrate prey to feed nestlings. When provisioning young, song thrushes foraged in habitats with higher invertebrate biomass than other habitats, with the exception of permanent pasture. The proportion of set-aside surrounding a skylark nest site was positively correlated with chick growth rate. However, higher proportions of araneae in skylark chick diets were shown to negatively correlate with chick growth, despite araneae being highly selected for from invertebrates available at foraging sites. Skylark nests that fledged young had higher growth rates than chicks in nests that failed.

In conclusion, this thesis revealed similarities in the pattern of nest site selection that were analogous to those of several other studies (skylarks – Donald et al., 2002a; yellowhammer – Stoate et al., 1998; Bradbury et al., 2000; MacCleod, 2001; Biber, 1993c; song thrush – Schnäck, 1991), foraging habitat use (skylarks – Chamberlain et al., 1999a; Wilson, 2001; yellowhammers – Stoate & Szczur, 1997; Morris et al., 2001a; Morris et al., 2001b; MacCleod, 2001) and chick diet (skylarks – Donald et al., 2001d; Jenny, 1990a; Poulsen et al., 1998; song thrush – Gruar et al., 2003). Results from this thesis provide evidence to support Odderskaer et al. (1997) and Morris et al. (2001b) in that skylarks forage in areas with sparser vegetation within winter cereals but not that they forage in areas with higher invertebrate abundance. Results from this study suggest that bird species with different ecological requirements could benefit from habitat management practices (inclusion of non-cropped and semi-natural habitats) that will increase heterogeneity on a farm and field level.

7.3 Conservation implications and recommendations

7.3.1 Agri-environment schemes: the future

As previously discussed, agricultural intensification has played an undisputed role in the decline of many farmland bird species (Fuller et al., 1995; Siriwardena et al., 1998a; Aebischer et al., 2000; Fuller, 2000; Donald et al., 2001c; Benton et al., 2003). The resulting formation of a relatively homogenous habitat landscape across the UK in the last 30 - 40 years has been detrimental to much wildlife (birds – Chamberlain & Gregory, 1999; Aebischer et al., 2000; invertebrates – Aebischer, 1991; Campbell et al., 1997; wild plants and their seeds – O'Connor & Shrubbs, 1986; Sotherton, 1998; Benton et al., 2002; and mammals - Flowerdew, 1997).

Over the last ten years, the introduction of agri-environment schemes, which effectively pay farmers to conserve the countryside, has helped to combat some of the effects of intensification on small and localised scales across Britain. Targeted agri-environment schemes in the UK have been shown to benefit some bird species (Aebischer et al., 2000), but in order to help reverse the declines of other species, more radical application of the available schemes is required. Currently the Countryside Stewardship Scheme (CSS) and the Environmentally Sensitive Areas (ESA) schemes, under the England Rural Development Programme, are

the most well funded agri-environment schemes available (see Chapter 1, section 1.5.1), receiving £51million and £48million of the £189.4million budget respectively. Eight other smaller schemes, each of which receives considerably less funding, are available to farmers and landowners across England (see Chapter 1). However, one of the main limitations of the CSS, available outside ESA areas, is that 20% of all applications cannot be funded due to budget limitations (Curry, 2002). These current agri-environment schemes are intensive and tailored to specific farms but more importantly, do not cover the whole country. Since a new farming 'culture' is developing, whereby conservation is generally becoming more accepted within the farming community, farmers are more understanding of the crisis facing wildlife on farmland (MacDonald & Johnson, 2000; Stoate, 2002). Farmers are more likely to participate in simple agri-environment schemes that require little effort for subsidies. However, MacDonald & Johnson (2000) also report that many farmers are concerned with the 'neatness' of the farm and perceive a 'tidy' farm as a mark of a good farmer and uncropped areas as a waste of land. Therefore implementing beneficial farmland practices to increase habitat heterogeneity and biodiversity may depend on further changing farmers attitudes to looking after the countryside.

In addition to the changing attitudes of farmers, it is likely that within the next few years, production-linked payments through the Common Agricultural Policy (CAP) will be substantially reduced. As farmers will need to recoup some of these direct payment losses, receiving payment for implementing agri-environment schemes could do this. Currently modulation is a voluntary mechanism, which allows member States of the EU to redirect a proportion of direct payments (up to 20%) into Rural Development Programmes (RDP) and agri-environment schemes. The EU finances direct payments, but RDP regulations are met half by the EU and half by the government and help pay for the England RDP. The UK planned modulation rate for 2003 and 2004 was 3.5% (Curry, 2002). Following the Curry review of UK policy (Curry, 2002), recommendations were made to the Government that suggested setting up a single agri-environment scheme for the future to encourage a 'whole farm' approach across the country. The Entry-level Scheme (ELS) is currently being piloted in a study covering four areas of England; Lincolnshire (arable cropping and horticulture), Devon (pastoral), County Durham (upland) and Berkshire (mixed) encompassing all types of farming and a range of farm sizes (Anon, 2002). Each area encompasses 100 farms.

If the pilot study is a success it is envisaged that the ELS will be fully introduced as the 'Environmental Stewardship Scheme' (ESS) in 2005. The ESS will comprise two levels, the 'Entry level' (ELS) and the 'Higher level' (HLS), and will be made available to all farmers and landowners across the UK. After acceptance of a farm map and plan, detailed prescriptions, each worth a number of 'points', will be chosen and a certain number of points, per hectare, must be reached before qualifying for a set payment. Each 'Entry level' agreement will be for 5 - years, unlike the CSS 10 - year agreement, and payment will be annual. There will be no competition for the funding, unlike the CSS, and it has been suggested that a flat rate of £30 per hectare per year and £15 per hectare per year for extensively grazed upland areas will be paid to farmers entering the scheme (<http://www.defra.gov.uk>). Prescriptions under the ELS will be wide and numerous, including the inclusion of simple grass field margins, hedgerow management, buffer strips, field corner management and low input grassland management. The HLS of prescriptions will be set up above the ELS, and these are likely to encompass the existing suite of schemes such as the Farm Woodland Premium Scheme, CSS and ESAs. HLS agreements will run for 10 - years, with a five-year break clause.

The ESS will be pivotal in maximising the delivery of habitat heterogeneity across the UK on a large scale, mainly because a larger number of farmers will be able to participate in future regardless of where their farm is situated. It therefore has the potential to successfully combine both perceived 'intensive' and 'non' intensive farm management, whilst rewarding farmers for their efforts. The resulting heterogeneity will cover all spatial scales (region, farm, within field), increase biodiversity and help the Government meet its targets for reversing the declines of farmland birds by 2020. However, a regular evaluation of the effectiveness of all agri-environment schemes is required to examine and assess whether they are having the desired effects on biodiversity (Kleijn and Sutherland, 2003).

7.3.2 Species specific recommendations

The results of the current study suggest that a number of measures to increase habitat heterogeneity could be taken to conserve skylarks, yellowhammers and song thrushes on lowland farmland in the UK. These will also benefit many declining invertebrate and plant species that they utilise. Key results specific to each species are emphasised and the ways in which the requirements of each species could be met through current and future

agri-environment schemes are discussed (using MAFF, 2000; Anon, 2002). A further section on how integrated management could benefit the study species together follows this.

7.3.2.1 Skylarks

- Set-aside was shown to be important for nesting
- Nests were situated in areas with more perennial grass cover and less dicotyledonous cover
- Nests that fledged young had higher growth rates than those that did not fledge young
- Nest sites were established around set-aside more than expected. Set-aside was also an important habitat when provisioning nestlings
- Areas with less crop cover and more bare ground in winter cereals were used for foraging
- Adults selected insect larvae and araneae to feed nestlings from foraging sites
- Chick growth rates increased with increasing proportion of set-aside around the nest
- Increasing proportions of araneae in nestling diet were associated with low nestling growth rate
- Low post-fledging survival rates were found. Most tagged chicks were predated whilst flightless.

Skylarks at Loddington clearly benefited from the provision of managed set-aside, spread out around the farm rather than being placed in blocks, for both nesting and foraging (Chapter 2, 3). This study is the first to document the positive aspects of managed set-aside strips for this species. As farmers do not receive further payment to manage set-aside, its inclusion (particularly under Wild Bird Cover) as an option in the future ELS is an important consideration. Additional payment could be received over and above the set-aside payment for farmers who invest time in managing it for wildlife. Wildlife mixtures, developed from the Wild Bird Cover crops, were included in the CSS from 2002, but payment can only be received when new habitats are created. Farmers who have previously put them in using their own funds are often not eligible.

The results of this thesis indicate that nesting birds would benefit from the provision of suitable *nesting* habitats within close proximity to preferred foraging habitats (Chapter 2, 3). Skylark nest sites contained more perennial grass and less dicotyledonous species cover than control sites within the same habitat (Chapter 2). The creation of beetle banks, which are planted with tussocky grasses such as cocksfoot (*Dactylis glomerata*)

and timothy (*Phleum pratense*), would provide suitable nesting habitats and can be created with CSS grants. Beetle bank structures do not sustain many dicotyledonous species, which strengthens their suitability as a nest site habitat, and are compatible with increasing the invertebrate abundance of potential skylark chick food invertebrates. Grass margins would also provide suitable nest site structures and could be positioned along a farm track next to a low hedge or the adjacent crop edge.

Provisioning skylarks may also benefit from an array of non-cropped habitat types, either developed on set-aside (e.g. Wild Bird Cover crops) or under CSS (e.g. Wildlife mixtures) (Chapter 3), particularly as the proportion of set-aside around a skylark nest was shown to have a significant positive influence on chick growth rates (Chapter 5). Grass margins and beetle banks harbour chick food invertebrates and provide a degree of shelter and protection to foraging birds. Skylarks are known to avoid field boundaries so the provision of non-cropped habitats is most likely to benefit this species when put in mid-field strips or, if necessary, next to a low hedge. Habitat diversity can be further increased by establishing several strips, each at least 6m wide, of different crop mixtures next to one another (as demonstrated at Loddington). For example, under CSS a 2m wide beetle bank could border the arable crop edge on one side, a 'Wild Bird Seed' mixture (containing 3 or more seed-bearing crops – kale, quinoa and cereals) on the other and alongside that a 'Pollen and Nectar' mix (with at least 4 nectar rich plants and 4 non-competitive grasses on the other) possibly bordering a grass track. The mosaic of these diverse habitats, with their heterogeneous sward structures and management, limiting pesticide and fertiliser use, would serve to provide skylark nest sites and invertebrate food throughout the breeding season and might possibly lengthen it. Easy to find, access and handle food items within the above options may help fledglings reach independence and increase their over-winter survival (Chapter 6). Currently, farmers are paid £510/ha/year for wildlife mixtures, as they are expensive to establish and require intensive maintenance, unlike grass margins (payment is £12/m/yr or £32/m/yr when in conjunction with a conservation headland) or beetle banks (£12/100m/yr) (MAFF, 2000; Anon, 2002).

Farmers often resist putting in mid-field strips since they break up large fields, take longer to service than large fields, have the potential to cause compaction around the field edges due to extra turning and there is a perceived risk of the spread of weeds into the crop edge. Where resistance is met, farmers should be

encouraged to put in strips extending out from a hedge. A degree of flexibility as to where each of the habitat prescriptions could be established is required.

Provisioning skylarks were shown to forage in areas of winter cereals with more bare ground and less crop (Chapter 4). It is suggested that the further development of wide row spaces (Morris et al., 2003) will benefit this species. However, whether wide row spacing (approximately 22cm apart) significantly affects crop yield is still being researched. Evidence to date shows no effects on yield when compared to yields from conventional spaced rows, up to row width of 22cm (Tillet et al., 1999; Tony Morris, results from SAFFIE project, pers. comm.). It is feasible that an arable field could be sown conventionally with a few lines being sown at wide row spacing mid-field. This would serve to increase weed abundance between row spaces (and hence increase invertebrate abundance) and possibly provide suitable nesting sites throughout the season. Ground movement of birds through the crop would be easier than within a conventionally sown crop later in the season, as long as the weeds were not too prolific. It is anticipated that the crop might be used more for foraging (than conventional row spacing), particularly if the invertebrate abundance also increased. Experiments at Loddington involving herbicides and double row spacing ('weed windows') are investigating the 'acceptable' weed level to farmers within a field (Alastair Leake/Chris Stoate pers. comm.). Thus, the possibility of wide row spacing may be a feasible option to include in the new ELS in the future. The sowing of spring cereals would provide a less dense foraging and nesting habitat, but currently there is only one agri-environment scheme prescription that promotes their use ('over winter stubbles' within the CSS), although several options within the ELS will be widely available. Despite this, certain soil types, for example heavy clay soil, remain unsuitable for the sowing of spring cereal crops whereas the adoption of wide row spacing may be an alternative option.

To increase the attractiveness of a cereal crop to skylarks during the breeding season, an alternative to wide row spacing would be to provide 'patches' void of sown crop within the crop. Skylark patches or 'scrapes' are currently being trialled by the RSPB Sustainable Arable Farming for an Improved Environment project (SAFFIE) (Morris et al., 2003). Their positive preliminary results suggest the breeding season is lengthened by the provision of these spaces, consistent with experimental work carried out by Odderskaer et al. (1997) in Denmark, leaving unplanted areas within the crop. Skylark nests within patches could potentially be exposed

to greater predation pressure, than those within wide rows, since the possible association of nests with patches across fields could alert predators to those nests. Nests in crops sown in wide rows may stand a greater chance of escape from predation since a predator would have to search either the whole field for a nest or the part sown in this way. However, few nests were found in crops sown with wide rows in the SAFFIE project, although nest survival rates were high (Morris et al., 2003). Research by Donald et al. (2002a) demonstrated that skylarks nesting next to tramlines later in the season suffered a high rate of predation from predators walking along these lines because crop density had increased. The provision of wide row spacing may possibly decrease this risk because birds have the opportunity to nest within the crop throughout the entire breeding season. In winter cereals skylark fledglings were most often found on bare ground within tramlines, potentially increasing their predation risk (Chapter 6). Wide row spacing may therefore help skylark fledglings reach independence, giving them a greater chance of survival. More simultaneous research on the provision of wide rows and patches within crops is required, although 'skylark plots' are already available under the pilot ELS options.

Skylarks selected insect larvae to feed their chicks (Chapter 5), some of which can be highly susceptible to insecticides (Sotherton, 1991). The provision of tussocky grassy margin habitats and beetle banks would serve to increase insect larvae. They harbour tipulidae, lepidoptera and many other invertebrates, such as coleoptera, that move into adjacent crops during the breeding season (Thomas et al., 1991, 1992a) and play an important role in skylark nestling diet. Skylarks are therefore also likely to benefit from 'Pollen and Nectar' mixes in the CSS, as adult lepidoptera will use this habitat (Feber et al., 1996) and could provide lepidoptera larvae in the summer.

When planning to provide non-cropped habitats, with the aim of increasing the abundance of invertebrates that comprise a large part of chick diet, it is important to determine how those chick food invertebrates affect nestling growth. For example, this study found a negative association of spiders with nestling growth rate, indicating that they not optimal prey (Chapter 5). Although it is not understood why this is so, purely providing habitats that serve to increase spider abundance, simply because they are fed to chicks in high quantities, may actually be detrimental to the chicks. This could provide further support for the argument to increase a variety of non-cropped habitats across a farm, thereby increasing invertebrate diversity, abundance

and potential accessibility across the season. However, Loddington, a demonstration farm, already has these habitats in place. The fact that skylarks were selecting some invertebrates negatively correlated with chick growth may be an indication that (i) the provision of the correct habitats to increase beneficial skylark chick food invertebrates is not being met, or (ii) that beneficial skylark chick food is present but birds cannot gain access to it, possibly due to vegetation structure. The view that dietary requirements were not being met at Loddington may be further supported by the fact that skylarks fed nestlings with grain, which is not documented in other studies (Chapter 5).

7.3.2.2 Yellowhammers

- Field margins were important nesting habitats
- Habitat availability around the nest did not influence nest survival rates
- Cereals were most important to breeding and provisioning adults, but beetle banks and crop set-aside types were also important when nesting
- Insect larvae and diptera were fed to the majority of broods, although adults selected insect larvae and araneae to feed nestlings from invertebrates available at foraging sites.

The results of this thesis suggest that hedgerow and ditch management under the CSS or ESAs (payment of £3/m) (MAFF, 2000) would benefit yellowhammers by providing suitable *nest* sites (Chapter 2). After the Second World War hedgerows were removed, causing a massive decline in this habitat (Barr & Parr, 1996). Since 1989 grants have been available to plant and restore hedgerows in many parts across the country and this is known to have increased bird abundance and diversity (O'Connor & Shrubbs, 1986; MacDonald & Johnson, 1995; Parish et al., 1995; Sparks et al., 1996). Other studies have shown that hedgerow height and width can affect which bird species will use it (Arnold, 1983). For example, Fuller et al. (2001) show yellowhammers prefer intermediate hedgerow heights, whilst Green et al. (1994) show yellowhammers prefer short hedgerows with few trees. Although results are often different, perhaps reflecting the local study sites, they demonstrate the need for a variety of hedgerow heights across a farm. The 'Enhanced Hedgerow Management' option under the ELS takes this into account. Another positive result from good hedgerow management is that

hedgerows harbour an abundant variety of invertebrates that will move out into field boundaries and crops (Thomas & Marshall, 1999), providing a resource of chick food close to nests.

In addition, the complementary development of herbaceous or grassy field margins adjacent to the hedgerows ensures the availability of high quality *nesting* and *foraging* habitats (Chapter 2, 3), which have the bonus of creating insect rich areas close to the nest site and increase plant and sward diversity (Wilson & Aebischer, 1995). Wide field margins serve to protect the hedge and its base from spray drift, which can have serious consequences for the invertebrate community, and therefore have a knock-on effect on the local bird populations. Wide field margins also take out the most unproductive part of the crop (Chaney et al., 1999), so farmers are more likely to consider putting a prescription for them in place when choosing prescriptions under the ELS. Field margins under CSS or ESAs can be sown with tussocky grasses or wild flowers to attract nectar-feeding insects, require minimal cutting and receive no herbicide treatments. 'Field Corner Management' under the ELS also takes unproductive and awkward field corners out of cultivation, helping to increase invertebrate abundance and create good foraging habitat for yellowhammers and other birds.

A number of management options that may benefit yellowhammers are similar to those discussed in section 7.3.2.1 for skylarks. Managed set-aside, laid out in strips, was common around yellowhammer nests and was a preferred foraging habitat whilst provisioning young (Chapter 3). The inclusion of cereal-based mixes, either under set-aside Wild Bird Cover option, or within the CSS as a Wildlife Seed mix, may benefit this species, particularly as they were shown to regularly feed their young both grain and invertebrates (Chapter 5). The 'Pollen and Nectar' mix may provide lepidoptera larvae, a component of nestling diet. Although cereal crops are important to yellowhammers around the nest site (Chapter 3) they contain lower invertebrate abundances than non-cropped habitats (Moreby & Aebischer, 1992). Yellowhammers foraged in patches of winter wheat with fewer invertebrates, particularly fewer araneae, than skylarks, suggesting that the importance of this crop to yellowhammers is for grain rather than invertebrates (Chapter 4). Therefore, in contrast to the skylark, cereal-based mixes would be better placed in strips, greater than 6m, alongside a hedge or along a farm track rather than mid-field. The provision of Wildlife Seed mixtures may help increase over winter survival of first year birds, since there would be more food available to them within their natal sites. Grassy margins and

conservation headlands under the CSS would also help increase potential yellowhammer chick food items, and increase available foraging habitat abundance and quality.

Double width rows in cereal crops may allow yellowhammers easier access to the ground. Like the skylark, manoeuvrability would be increased, as would the accessibility of invertebrates. Yellowhammers are more likely than skylarks to include seeds in nestling diet, so the increase in arable weeds between rows may further supplement the diet. As for the skylark, insect larvae and araneae were important constituents of yellowhammer nestling diet (Chapter 5). Habitats that will help increase these invertebrate numbers are beetle banks, field margins, wildlife mixtures and conservation headlands, all of which are funded under CSS, some ESAs and the new ELS.

Yellowhammers were shown to avoid permanent pasture when provisioning chicks at Loddington (Chapter 3). The 'low-input' grassland management prescription (receiving low inputs of fertiliser and herbicides) within the ELS may help restore this habitat as a potential food source by increasing invertebrate chick food during the breeding season (Vickery et al., 2001). A move towards a mixed farming regime for yellowhammers, including the availability of grazed pasture, may serve to improve habitat heterogeneity at a territory and farm level.

7.4.2.3 *Song thrushes*

- Boundary habitats, particularly hedgerows, and woodland were important for nesting
- Habitat availability influenced nest survival rates. The proportion of permanent pasture positively influenced nest survival during the incubation stage. Nest survival rates during incubation decreased when nests were built on the border of the farm and when predator control was not taking place. Nest survival during the nestling stage was affected by the month in which nestlings occupied the nest, being lower in May and August than in April and June, and by the nest site habitat, with nest survival rates being highest in woods and hedgerows.
- Boundary habitats and woodland were important to breeding birds. Arable crops, permanent pasture and set-aside were generally avoided when provisioning nestlings.

- Earthworms, slugs and snails comprised the majority of nestling diet.
- No habitat, environmental or dietary effects were detected with regard to song thrush chick growth rates.

The results of this thesis demonstrate that breeding song thrushes might benefit from the planting and restoration of hedgerows and ditch maintenance under the CSS, thus providing *nest sites* and *feeding grounds* (Chapter 2, 3). The encouragement of herbaceous vegetation along ditch and field margins bordering hedgerows and along riparian habitats, such as ponds and streams, is likely to keep the ground damper for a longer period throughout the breeding season, perhaps leading to the extended availability of earthworms. In addition, there are several options within the ELS for field boundary, tree and woodland management that could benefit song thrush nesting and foraging opportunities.

Cereal crops generally have poor earthworm abundances (Tucker, 1992), and this may have been reflected in their avoidance by provisioning song thrushes (Chapter 3). Since song thrushes favoured boundary habitats, the provision of grass margins bordering cereal crops and woodland edges, which are likely to increase worm availability, could be beneficial (Chapter 3). Surprisingly, permanent pasture was not strongly selected by adults with nestlings, despite it holding high soil invertebrate biomass (Chapter 3, 4). However, increasing proportions of permanent pasture around the nest positively influenced nest survival rates during incubation (Chapter 2), possibly as it allowed incubating females to reduce their time spent away from the nest while foraging. The provision of permanent pasture for breeding song thrushes is therefore important. Mixed farms, with relatively small field sizes, mixed arable crop rotations providing a patchwork of crop types, hedgerows and uncropped habitats, will benefit this species. The inclusion of 'low-input' grassland management, as an option within the ELS, may prove beneficial to this species, particularly if it is provided alongside woodland or hedgerows, as it could increase earthworm abundance. There are no long-term abundance trends on earthworms on farmland (Wilson et al., 1999) but cultivations, use of insecticides and fertilisers, the loss of grassy margins and other non-cropped habitats are likely to reduce abundances. Earthworms are susceptible to a range of synthetic pesticides, such as carbamate insecticide, carbendazim fungicides and molluscides (Edwards, 1984). Inputs such as lime tend to increase earthworm populations and larger doses of nitrogen reduce them (Edwards & Lofty, 1977). Selective pesticide and fertiliser use will therefore benefit the song

thrush in conjunction with habitat management. Likewise, earthworm abundances may be increased with the controlled application of farmland manure (Edwards & Lofty, 1982; Scullion & Ramshaw, 1987), increasing organic food supplies (Edwards and Lofty, 1972).

Woodland was shown to be an important habitat for both *nesting* and *foraging* throughout the breeding season (Chapter 2, 3). Current agri-environment schemes promoting woodland and scrub, such as the Farmland Woodland and Premium Scheme and the Woodland Grant Scheme that provide grants to either convert agricultural land to woodland or to create new woodlands and manage them correctly, will be advantageous to song thrushes. These schemes will form part of the HLS of the new ESS. Song thrushes often nested in conifers. Conifer plantations grow quickly. The trees themselves offer a good degree of camouflage throughout the whole breeding season so could potentially help to build up the song thrush population on a specific site in conjunction with other habitat management schemes, such as interspersed planting of broadleaved tree species. Earthworms are an important component of chick diet (Chapter 5) and the damp conditions that often accompany ditches and broadleaved woodland floors are likely to encourage earthworm actively close to the soil surface. Increased drainage has caused the loss of meadows and damp fields (Fuller et al., 1991) so agri-environment prescriptions aimed at raising water levels, particularly in permanent pasture and grassland habitats, will help increase the availability of earthworms near the soil surface and possibly increase its attractiveness to provisioning thrushes.

7.4.2.4 Implications for all three species

As discussed, skylarks, yellowhammers and song thrushes are likely to benefit from many of the current and future agri-environment schemes, particularly because the introduction of habitats created through these schemes leads towards less intensive farming habitats beneficial to many farmland birds (Siriwardena et al., 2001). Targeted prescriptions placed around the farm to encourage one bird species will be advantageous to others, possibly at different times of the year and for different reasons. For example, blackbirds (*Turdus merula*) appeared to avoid set-aside during the summer months at Loddington but were frequently seen utilising kale set-aside to forage in the winter (pers.obs).

Set-aside and agri-environment schemes have been in operation for over 15 years. Set-aside became the third largest land use, after grass and cereals on lowland farmland in the UK (Sotherton, 1998). In addition, 22 ESAs covered 10% of agricultural land involving 9300 agreements, covering 474000ha, and 7400 CSS scheme agreements were in place by the end of 1997 (Ovenden et al., 1998). As a result, habitat heterogeneity has clearly increased and has fulfilled numerous roles within the life cycles of a range of bird species but on a small spatial scale since not all applications are funded. This may be one of the reasons Fuller (2000) states that, despite some beneficial management (e.g. the provision of large areas of set-aside and more oilseed rape being grown), some bird species are still declining and that 10 declining species still had to reach their new carrying capacity (including the skylark and yellowhammer). Indeed, whether a particular species population is increasing or decreasing may reflect habitat availability and quality. More can be carried out to provide attractive and useable habitats to many species across the country on a wider spatial scale and the ESS is the first agri-environment scheme that aims to do so. After much speculation regarding the phasing out of set-aside by 2000, it is still conditional for arable area payment eligibility until 2005. From 2005, 6-10m strips around field margins will be permissible (www.andersons.co.uk). Current set-aside rules and regulations can, however, be detrimental to nesting birds and non-rotational set-aside can be cut as early as 15th July when skylarks and yellowhammers are nesting. Several authors have suggested that this date should be changed to at least the 1st August when most nesting attempts will be completed (e.g. Brickle, 1999; Donald, 1999) and from 2005 the new set-aside period will run from January 15th to September 1st (www.defra.gov.uk).

Despite the potential for set-aside and new agri-environment schemes to help reverse farmland bird declines, their effects will not be immediate (Fuller, 2000; Chamberlain et al., 2000a). Nevertheless, there are other systems in place that also improve heterogeneity on farmland habitat that are not compulsory or payment driven. Siriwardena et al. (2000c) demonstrated that, at the territory scale, yellowhammers have higher reproductive success on mixed farms than arable or pastoral farms. Diverse, and well distributed, cropping systems that incorporate break crops and pasture will benefit many species. Birds are likely to work less hard to feed their young, probably reducing reproductive effort on their part and possibly improving their survival.

Organic farming methods, with reduced pesticide and fertiliser applications, may also benefit many of the chick food invertebrates and several studies have demonstrated the positive aspects of this farming regime for

farmland birds (Booij & Noorlander, 1992; Peterson, 1994; Wilson et al., 1997a; Chamberlain et al., 1999b; Freemark & Kirk, 2001). Nonetheless, unless vast proportions of the farming community change to an organic system, benefits of this regime will be localised. Farmland management practices that will increase key invertebrate populations will benefit farmland birds (Benton et al., 2002). Extensification, minimum tillage and direct drilling are other farming practices that increase both arable weeds and seeds and soil invertebrates whilst encouraging a move away from intensification. Earthworms benefit from the lack of soil disturbance (Edwards, 1975; Edwards & Lofty, 1982; Edwards, 1984) and an increase in the use of minimum tillage instead of conventional ploughing, due to economic pressures (Jordan et al., 2000), may make it an attractive option to many farmers. The use of minimum tillage could be further incorporated into the ELS in the future, as presently it is only included in one option to reduce cultivation depth on land where there are archaeological features.

Although predation was shown to be the main cause of nest failure for all three species, it remains unlikely with the current economic state of farming and social structure within Great Britain that predator control will ever occur over a large scale. Many areas managed for shooting carry out small-scale predator control but it will never reach the same levels as pre-war Britain, particularly as such control remains the subject of an ongoing and very sensitive debate. Despite this, the role of habitat management carried out by farms that hold shoots is widely recognised (MacDonald & Johnson, 2000; Mead, 2000). To investigate whether predator control alone affects nest survival and breeding productivity, current research at Loddington aims to see whether the absence of predator control, when all habitat requirements are met, influences breeding success of a range of farmland bird species.

7.4 Future research needs

This study illustrates how understanding habitat use and habitat preferences, with regard to chick diet and vegetation structure at foraging sites, can be invaluable for helping to determine sympathetic management practices relating to factors affecting foraging by breeding farmland birds. However, the research in this thesis recognised a number of issues that require further study. The main issues are identified as:

1. A more detailed examination of nest site specifics is required, e.g. song thrush nest placement in hedgerows, to identify factors that can be actively managed to enhance nest sites and increase breeding success, such as supporting species, structure, height and positioning. A study such as this would further identify factors important to breeding birds, which could well be managed.
2. Examination of the microhabitat of song thrush foraging sites, starting with a coarser scale than was used in the current study when determining habitat use and working towards a finer scale. For example, investigating earthworm availability within each habitat type available across the farm landscape and determining changes in earthworm availability that is experienced over the course of a breeding season. Alongside this, examination of vegetation structure and soil penetrability changes within each of these habitat types across the season is needed. It is likely that telemetry is not the best tool to investigate such precise, and intense, locations of habitat use unless backed up by sightings of the bird. Fewer fixes should therefore be taken across the day and the bird could be flushed from its habitat once each fix is completed. A project such as this may better investigate whether provisioning song thrushes are influenced by invertebrate availability or vegetation structure.
3. Further development of the skylark post-fledging study, with regard to the use of radio-tags, chick survival and habitat use. For this to be possible tag life must be extended and a larger sample size achieved. Whole broods could be tagged to gather estimates on brood survival to post-fledging. A study such as this could help to identify management practices that could increase post-fledging survival, including the use of wide row spacing, and provide better estimates of survival.
4. Further examination of the effect of skylark chick growth rates during the nestling period, by following the development of many broods, collecting individual growth rate measurements and chick diet samples (faecal or neck ligatures), and tagging all individuals prior to fledgling. Whether

nestling growth rates affects post-fledging survival could be investigated in detail to see whether heavier chicks, or those with higher growth rates, do survive to independence. Alongside this, an examination of skylark fledgling diet, to see how it changes when reaching independence, would be appropriate, to examine whether diet changes as they become independent. Faecal samples could be collected and assessed from nestlings and tagged fledglings from the same brood.

5. Araneae were highly selected invertebrates fed to nestlings that had a negative association with growth rates. As decreased growth rates can influence successful fledging or survival an investigation into nestling diet and the effect of specific invertebrate groups on skylark, yellowhammer and song thrush chick growth would be beneficial. This investigation could be combined with a study into the calorific value of highly selected invertebrate groups, so that habitat prescriptions could be aimed at increasing the 'more nutritional' selected invertebrates and aim to make them accessible for birds.
6. A more accurate assessment of invertebrate availability to provisioning birds would be required through a combination of D-vacuum sampling, pitfall trapping and sweep netting.
7. Ideally Loddington should be paired with two similar sized farms with no/few habitat management prescriptions and similar conditions to provide comparisons. Results from a study such as the one carried out during this thesis should be able to help distinguish genuine benefits of habitat management. Baseline data should be collected from the two comparison sites before implementing the recognised habitat management at one of the sites only. A second investigation should be carried out in a few years to see whether habitat management benefits to birds were identified, and comparable, with results from Loddington.

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Appendices

1.1 Latin names of the flora found within botanical species quadrats at Loddington, or used in the text.

Latin name	English name	Annual/perennial spp.
<i>Poa annua</i>	Annual meadow grass	Perennial grass
<i>Helianthus tuberosus</i>	Artichoke	
<i>Hordeum sp.</i>	Barley sp.	
<i>Anisantha sterilis</i>	Barren brome	Annual grass
<i>Phaseolus sp.</i>	Beans	
<i>Fallopia convolvulus</i>	Bindweed	Perennial dicotyledon
<i>Lotus corniculatus</i>	Birdsfoot trefoil	Perennial dicotyledon
<i>Alopecurus myosuroides</i>	Black grass	Perennial grass
<i>Prunus spinosa</i>	Blackthorn	
<i>Borago officinalis</i>	Borage	Annual dicotyledon
<i>Rubus fruticosus</i>	Bramble	Perennial dicotyledon
<i>Rumex obtusifolius</i>	Broadleaved dock	Perennial dicotyledon
<i>Sinapsis arvensis</i>	Charlock	Annual dicotyledon
<i>Stellaria media</i>	Chickweed	Annual dicotyledon
<i>Galium aparine</i>	Cleavers	Annual dicotyledon
<i>Trifolium sp.</i>	Clover	Annual dicotyledon
<i>Dactylis glomerata</i>	Cock's foot	Perennial grass
<i>Elytrigia repens</i>	Common couch	Perennial dicotyledon
<i>Taraxacum officinale</i>	Common dandelion	Perennial dicotyledon
<i>Urtica dioica</i>	Common nettle	Perennial dicotyledon
<i>Atriplex patula</i>	Common orych	Annual dicotyledon
<i>Anthriscus sylvestris</i>	Cow parsley	Perennial dicotyledon
<i>Geranium sp.</i>	Cranesbill sp.	Annual dicotyledon
<i>Ranunculus repens</i>	Creeping buttercup	Perennial dicotyledon
<i>Cirsium arvense</i>	Creeping thistle	Biennial dicotyledon
<i>Cynosurus cristatus</i>	Crested dog's tail	Perennial grass
<i>Oenothera biennis</i>	Evening primrose	Perennial dicotyledon
<i>Arrhenatherum elatius</i>	False oat	Perennial grass
<i>Chenopodium alba</i>	Fat hen	Annual dicotyledon
<i>Viola arvensis</i>	Field pansy	Annual dicotyledon
<i>Myosotis arvensis</i>	Forget-me-knot	Annual dicotyledon
<i>Epilobium hirsutum</i>	Great willowherb	Perennial dicotyledon
<i>Senecio vulgaris</i>	Groundsel	Annual dicotyledon
<i>Hieracium sp.</i>	Hawkweed	Perennial dicotyledon
<i>Crataegus monogyna</i>	Hawthorn	
<i>Galeopsis sp.</i>	Hemp nettle	Annual dicotyledon
<i>Heracleum sphondylium</i>	Hogweed	Perennial dicotyledon
<i>Brassica napus</i>	Kale	Biennial dicotyledon
<i>Centaurea nigra</i>	Knapweed	Perennial dicotyledon
<i>Polygonum aviculare</i>	Knot grass	Annual dicotyledon
<i>Linum usitatissimum</i>	Linseed	Annual dicotyledon
<i>Malva sylvestris</i>	Mallow	Perennial dicotyledon
<i>Tripleurospermum inodorum</i>	May weed	Annual dicotyledon
<i>Avena sativa</i>	Oat sp.	
<i>Brassica napus</i>	Oilseed rape	
<i>Chrysanthemum leucanthemum</i>	Oxeye daisy	Perennial dicotyledon
<i>Lolium perenne</i>	Rye grass	Perennial grass
<i>Phaecelia tantacetifolia</i>	Phaecelia	Annual dicotyledon
<i>Plantago sp.</i>	Plantain	Perennial dicotyledon
<i>Chenopodium quinoa</i>	Quinoa	Annual dicotyledon
<i>Trifolium pratense</i>	Red Clover	Annual dicotyledon

<i>Lmium purpureum</i>	Red dead-nettle	Annual dicotyledon
<i>Festuca rubra</i>	Red fescue	Perennial grass
<i>Polygonum persicaria</i>	Red shank	Annual dicotyledon
<i>Chamerion angustifolium</i>	Rosebay willowherb	Perennial dicotyledon
<i>Poa trivialis</i>	Rough meadow	Perennial grass
<i>Bromus hordeaceus</i>	Soft brome	Annual grass
<i>Sorghum bicolor</i>	Sorghum	
<i>Sonchus oleraceus</i>	Sow thistle	Biennial dicotyledon
<i>Cirsium vulgare</i>	Spear thistle	Biennial dicotyledon
<i>Veronica sp.</i>	Speedwell	Annual dicotyledon
<i>Dipsacus fullonum</i>	Teasel	Biennial dicotyledon
<i>Phleum pratense</i>	Timothy	Perennial grass
<i>Triicale hexaploide</i>	Triticale	
<i>Vicia sp.</i>	Vetch	Annual dicotyledon
<i>Triticum aestivum</i>	Wheat	
<i>Sinapsis alba</i>	White mustard	Annual dicotyledon
<i>Avena fatua</i>	Wild oat	Perennial grass
<i>Pastinacea sativa</i>	Wild parsnip	Perennial dicotyledon
<i>Rhinanthus</i>	Yellow rattle	Annual dicotyledon
<i>Holcus lanatus</i>	Yorkshire fog	Perennial grass

1.2 Latin names of birds and mammals within the thesis

Latin name	English name
<i>Turdus migratorius</i>	American robin
<i>Meles meles</i>	Badger
<i>Tyto alba</i>	Barn owl
<i>Parus minor</i>	Blue tit
<i>Rattus norvegicus</i>	Brown rat
<i>Pyrrhula pyrrhula</i>	Bullfinch
<i>Fringilla coelebs</i>	Chaffinch
<i>Emberiza cirrus</i>	Cirl bunting
<i>Streptopelia decaocto</i>	Collared dove
<i>Miliaria calandra</i>	Corn bunting
<i>Crex crex</i>	Corncrake
<i>Corvus corone</i>	Carrion crow
<i>Felis felis</i>	Domestic cat
<i>Vulpes vulpes</i>	Fox
<i>Lepus capensis</i>	Hare
<i>Passer domesticus</i>	House sparrow
<i>Natrix natrix</i>	Grass snake
<i>Parus major</i>	Great tit
<i>Dumetella carolinensis</i>	Gray catbirds
<i>Perdix perdix</i>	Grey partridge
<i>Passer domesticus</i>	House sparrow
<i>Falco tinnunculus</i>	Kestrel
<i>Vanellus vanellus</i>	Lapwing
<i>Calamospiza melanocorys</i>	Lark buntings
<i>Sylvia curruca</i>	Lesser whitethroat
<i>Carduelis cannabina</i>	Linnet
<i>Pica pica</i>	Magpie
<i>Phasianus colchicus</i>	Pheasant
<i>Emberiza schoeniclus</i>	Reed bunting
<i>Alauda arvensis</i>	Skylark
<i>Turdus philomelos</i>	Song thrush
<i>Accipiter nisus</i>	Sparrowhawk
<i>Mustela erminea</i>	Stoat
<i>Columba oenas</i>	Stock dove
<i>Burhinus oedicnemus</i>	Stone curlew
<i>Streptopelia turtur</i>	Turtle dove
<i>Passer montanus</i>	Tree sparrow
<i>Mustela nivalis</i>	Weasel
<i>Sylvia communis</i>	Whitethroat
<i>Apodemus sylvaticus</i>	Wood mouse
<i>Columba palumbus</i>	Wood pigeon
<i>Hylocichla mustelina</i>	Wood thrush
<i>Emberiza citrinella</i>	Yellowhammer
<i>Junco phaeonotus</i>	Yellow-eyed juncos